FORAGING STRATEGIES AND SPECIES INTERACTIONS OF FOUR DEEP-SEA INVERTEBRATES FROM THE NORTHWEST ATLANTIC

by Brittney Stuckless

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Abstract

This study explored diets, foraging strategies, locomotor behaviours, and competitive dynamics in four abundant bathyal species from the Northwest Atlantic (the sea stars *Ceramaster granularis*, *Hippasteria phrygiana*, and *Henricia lisa*, and the gastropod *Buccinum scalariforme*). A combination of singleton trials, multi-animal trials, and simulated food fall experiments were conducted under cold, darkened laboratory conditions, using infrared-capable time-lapse recording. Feeding trials showed that scavenging is prevalent in all species studied. Frame-by-frame analysis of locomotor patterns revealed pulsing movement speeds in all species, an unreported but possibly widespread locomotor style for mobile benthic taxa. Multi-animal trials revealed a variety of cooperative and competitive behaviours in the focal species, altered by the number, size, and species identity of competitors. By combining singleton and multi-animal trials, this work provided data about how these species detect and assess potential food sources, and whether they can modify their foraging strategies or behaviour in competitive settings.

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about my animals and research for hours on end, despite only understanding half of what I was talking about, and always being available for support when I was struggling.

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Co-Authorship Statement

The research in this thesis and all the written work was completed by Brittney Stuckless under the guidance of Annie Mercier, with additional input from Jean-François Hamel. The data chapters are formatted as manuscripts for publication in scientific journals, with authorship as follows:

Chapter 2: Brittney Stuckless conceived the project, analyzed the data and wrote the manuscript with the help of Annie Mercier with key input from Jean-François Hamel. Jacopo Aguzzi provided intellectual and editorial input at the manuscript stage, and Scott Grant provided comments on the thesis version. Authorship of the manuscript derived from this chapter is: B. Stuckless, J.-F. Hamel, J. Aguzzi & A. Mercier.

Chapter 3: Brittney Stuckless developed the project ideas under the guidance of Annie Mercier and Jean-François Hamel, and collected and analyzed all the data. The chapter was written by Brittney Stuckless with suggestions and edits from Annie Mercier, Jean-François Hamel, Jacopo Aguzzi, and Scott Grant. Authorship of the manuscript being developed from this chapter will be: B. Stuckless, J.-F. Hamel, J. Aguzzi, & A. Mercier.

Chapter 1 General Introduction and Overview

1.1 Feeding ecology of deep-sea species

Despite being the largest environment on earth, the deep sea (generally beyond the shelf break, >200 m depth) and its biota remain largely understudied when compared to less remote shallow-water counterparts (Ramirez-Llodra et al., 2010). Basic knowledge of the ecology and biology of most deep-sea species, including some of the most abundant, is still lacking or incomplete (Hudson et al., 2004; Gale et al., 2013; Robertson et al., 2017; Danovaro et al., 2020).

Among key aspects, trophic levels, species-specific diets, feeding patterns, and intra/interspecific competition can contribute to a better understanding of the ecosystem roles and functions played by megafauna (i.e. animals larger than 1-2 cm; Rex et al., 2006). However, for ecosystems of the deep sea, such data are challenging to assemble even for ecologically relevant (abundant) sedentary benthic taxa (Ramirez-Llodra, 2002) because: (i) opportunities to collect or observe deep-sea species *in situ* are often spatially and temporally limited; (ii) organisms can be physically and biologically damaged by equipment, pressure, and temperature changes when collected and brought to the surface (rendering them unsuitable for studies); and (iii) maintaining deep-sea species under laboratory conditions requires unique infrastructure capacities (Shillito et al., 2001; Raymond & Widder, 2007). Hence, compared to the body of literature on shallow-water species from tropical (e.g. Behringer & Butler IV, 2006; Sardenne et al., 2017), temperate (e.g. Gagnon et al., 2003; Wong & Barbeau, 2003) and polar regions (e.g. Legeżyńska et al., 2012), data of this nature on deep-sea taxa are scarce. Nevertheless, some information has been gathered on diets and food webs through stable isotopes and fatty acids analyses and gut content analyses, (Gale et al., 2013; Stevenson & Mitchell, 2016; Drazen &

Sutton, 2017; Parzanini et al., 2018a, 2018b), and using photo and video observations of deep-sea species *in situ* (Choy et al., 2017). However, little exists on foraging strategies and species interactions when sporadic food supplies become available, such as food falls from the surface reaching bathyal or abyssal depths and/or recruitment pulses (outbreaks) of prey species (Klages et al., 2000; Premke et al., 2006; Bailey et al., 2007; Aguzzi et al., 2012).

1.2 Challenges associated with the study of deep-sea species

In general, obtaining baseline knowledge on feeding patterns, foraging strategies, and species interactions in deep-sea species is accompanied by unique challenges. Video and photo analyses have long been used by researchers to study animal behaviour; however, the cold, high-pressure and dimly lit (or completely dark) conditions of the deep sea, coupled with the frequently sparse occurrence of deep-sea organisms (outside of chemosynthetic environments) can present problems when trying to use such methods to record deep-sea species in their natural habitats (Shillito et al., 2001; Raymond & Widder, 2007). Remotely operated vehicles (ROVs) are a tool often used by researchers to observe deep-sea species in the field. For example, Raymond and Widder (2007) tested photosensitivity of two deep-sea species of fish (*Coryphaenoides acrolepis* and *Anoplopoma fimbria*) to various types of light (white, near-red and far red). ROVs have also been used to record how animals respond to food in the wild; for instance in a study by Higgs et al. (2014) which looked at scavenging around naturally occurring food falls in the south-east Atlantic off the coast of Angola. ROVs have also been used to record and sample populations of organisms such as polychaete worms around deep-sea hydrothermal vents for use in abundance and biomass calculations (Chevaldonné & Jollivet, 1993), and to gather photos and videos to assess specific behaviours in species of interest such as the carrying behaviour of the deep-sea crab *Paromola cuvieri* (Braga-Henriques et al., 2011). An alternative

method for recording deep-sea species *in situ* is the use of static cameras that are baited or placed at food falls. Such cameras allow researchers to see what types of animals are drawn to certain food sources (Jamieson et al., 2006; Premke et al., 2006; Bailey et al., 2007; Sweetman et al., 2014); however, natural food falls can be sparse and are often only observed opportunistically, whereas identifying the species present and their behaviours and interactions in a complex assemblage is challenging. In addition, the set up of baited cameras may exclude certain kinds of species that may have otherwise been attracted to the bait used (e.g. if the bait is suspended off the seafloor where benthic or infaunal organisms cannot easily reach it) and the resolution and/or field of view of images may make identifying the presence of smaller animals (such as whelks or sea stars) difficult or impossible (Klages et al., 2000; Premke et al., 2006; Raymond & Widder, 2007; Higgs et al., 2014).

While the above-mentioned types of studies have provided crucial information regarding species that are often difficult/costly to collect and house in laboratory environments, these methods also have some drawbacks. Chief among them is the fact that prolonged exposure to bright lights needed to illuminate camera fields may repulse some species, and/or generate unknown biases or damages to the sensory organs of observed species (Raymond & Widder, 2007; Aguzzi et al., 2011). In addition, ROVs are generally limited in both deployment times (anywhere from a few hours to a few days) and the surface area they can survey at a given time, and it has been suggested that movement or vibration from their operation may disturb animals and cause unnatural/incomplete behaviours to be recorded (Raymond & Widder, 2007; Trenkel & Lorance, 2011; Mallet & Pelletier, 2014).

Indirect methods based on serial collections of specimens, such as gut-content analysis provide a valuable alternative to *in situ* observations, although the feeding habits of a species

cannot be fully assessed due to potential temporal and biological biases, i.e. only the most recent meals or food items consisting of hard parts linger long enough in the digestive tracts. Additional issues arise with gut content analysis in animals like sea stars that may feed externally through everted stomachs (Gale et al., 2013). Isotopic analysis also provides valuable information on diet and overall trophic level (Stevenson & Mitchell, 2016; Drazen & Sutton, 2017; Parzanini et al., 2017, 2018b) but gives little to no insight into specific feeding behaviours or foraging strategies.

Observing deep-sea species in a laboratory setting permits a measure of control that is unobtainable in field studies, allowing researchers to limit the number of variables that may be influencing focal individuals (e.g. current speed and direction, presence or absence of other individuals, temperature). However, due to the difficulties of collecting intact deep-sea species and housing them in appropriate laboratory settings (e.g. maintaining low temperature, stable salinity, low light or dark conditions), many laboratory-based studies with live deep-sea species are performed within 48 h of collection or less (e.g. Shillito et al., 2001; Ravaux et al., 2003). In such cases, individuals may still be experiencing collection stress resulting from abrupt changes in pressure, temperature, or light levels (among other factors), or they may have been injured during collection; as such, these individuals may be behaving abnormally. Studies that used live, freshly caught individuals often focused on heat-shock responses or responses to changes in pressure, as these can be performed relatively quickly and on multiple individuals at a time (Shillito et al., 2001; Ravaux et al., 2003; Mestre et al., 2015). Laboratory studies on behaviours such as foraging, feeding, or competitive interactions typically require longer holding times to standardize individuals, e.g. harmonizing hunger levels (e.g. Rochette et al., 1994; Gale et al., 2013; St-Pierre & Gagnon, 2015; Sbragaglia et al., 2017; St-Pierre et al., 2018). As a result, few studies to date have documented the feeding preferences and behaviours, or the competitive

interactions, of deep-sea species after lengthy acclimation to a laboratory environment using experimental trials (Gale et al., 2013; Nuñez et al., 2016; Sbragaglia et al., 2017).

1.3 Background information

Much of the work on food acquisition or competition carried out to date on deep-sea taxa focuses on crustaceans and fishes (e.g. Laver et al., 1985; Klages et al., 2000; Premke et al., 2006; Würzberg et al., 2011; Yeh & Drazen, 2011; Nuñez et al., 2016; Drazen & Sutton, 2017). Among deep-sea echinoderms, most of the work regarding feeding thus far relates to holothuroids (Hudson et al., 2004; Hudson et al., 2005; Amaro et al., 2009), whereas comparatively little exists on other dominant echinoderms (e.g. sea stars), and on other important phyla such as molluscs (Lauerman, 1998; Aguzzi et al., 2012; Gale et al., 2013).

Competition is known to be an important factor influencing the behaviour of many species of shallow-water marine benthic organisms, as resources (e.g. food, space, mates) are typically limited in nature (e.g. Menge, 1972; Menge & Menge, 1974; Rogers et al., 2018). Factors such as body size, hunger state, and morphology can influence potential competitive interactions between individuals, whether of the same or differing species (Menge, 1972; Menge & Menge, 1974; Schmid & Schaerer, 1981), and the identity of a potential competitor may modulate the response of an individual to a competitive situation (St-Pierre et al., 2018). As the deep sea is typically a food-limited environment, competition over food resources is likely a driver of behaviour in deep-sea species (Yeh & Drazen, 2011; Aguzzi et al., 2018), however, very little work to date has been done specifically addressing potential dominance hierarchies in deep-sea ecosystems or species (Sbragaglia et al., 2017). While food falls (such as fish or whale carcasses) represent a large influx of a normally scare resource, and some work has been done to describe the sequence of food fall (or baited camera) occupation by deep-sea species, (e.g.

Klages et al., 2000; Premke et al., 2006; Yeh & Drazen, 2011; Aguzzi et al., 2012; Higgs et al., 2014; Sweetman et al., 2014) there is typically very little, if any, mention of competitive interactions between scavengers. Previous studies looking at the reproductive and feeding behaviours of deep-sea individuals under laboratory conditions that more accurately reflect their natural environment have been insightful (e.g. Mercier & Hamel, 2008; 2009; Sahlmann et al., 2011; Gale et al., 2013; Montgomery et al., 2017); thus, further work along similar lines is likely to be of great benefit when attempting to provide baseline information about these species.

1.4 Focal species

The species used in this study were chosen based on their availability and the existing knowledge base on relevant aspects of their biology, focusing on four abundant bathyal species in eastern Canada: the gastropod *Buccinum scalariforme*, and the sea stars *Ceramaster granularis*, *Hippasteria phrygiana*, and *Henricia lisa* (Figure 1.1). The whelk *B. scalariforme* is known to occur between subtidal and bathyal depths (>1100 m) in the Arctic as well as off Greenland, Iceland, Alaska (USA), the eastern and western coasts of Canada, and as far south as Maine (USA) (Montgomery et al., 2017). The sea star *C. granularis* is found at depths ranging from ~50 to >1400 m in the Arctic Ocean, including the coasts of Greenland and Iceland, along both coasts of the North Atlantic Ocean, and the Northeast coast of South America (Gale et al., 2015; Mah, 2019a). The sea star *H. phrygiana* is a widely distributed species found throughout the Northern and Southern Atlantic and Pacific oceans at depths ranging from 10-1400 m (Mah et al., 2014), whereas *H. lisa* is found in deep waters of the North Atlantic basin down to ~1400 m (Mah, 2019b).

The diet of shallow-water members of the genus *Buccinum* has been examined (Himmelman & Hamel, 1993; Evans et al., 1996; Ilano et al., 2005). In addition, limited work

has been carried out on two deep-sea whelk species, *Tacita zenkeyitchi* and *Buccinum yoroianum* (Aguzzi et al., 2012) and there was a brief mention of some scavenging tendencies of *B. scalariforme* in Montgomery et al. (2017). Studies exist that have assessed intraspecific and interspecific interactions involving shallow-water whelk species, or interactions between whelks and other taxa, such as sea stars (e.g. Brown & Alexander Jr, 1994; Morissette & Himmelman, 2000; Rochette et al., 2001), but none thus far pertain to deep-water counterparts such as *B. scalariforme*.

The diets of the sea stars *C. granularis*, *H. phrygiana*, and *H. lisa* have been explored through stable isotope and gut contents analyses (Mercier & Hamel, 2008; Gale et al., 2013; 2015). It has been suggested that *C. granularis* is a generalist sponge eater and may also prey upon corals to a degree, while analysis of stomach contents suggests that benthic foraminifera may also be a diet component (Gale et al., 2013; 2015). *H. phrygiana* is known to prey upon cnidarians and may engage in limited detritivory (Gale et al., 2013; 2015) but few other potential prey types have been investigated in the species. *H. lisa* is known to be a sponge eater based on *in situ* observations (Mercier & Hamel, 2008; Robertson et al., 2017), although whether the species feeds upon other types of prey is uncertain. Minimal work exists on species interactions or behaviour for any of these sea star species, as is the case for most deep-sea species, although species interactions have been investigated in shallow-water counterparts in regard to conspecifics, other species of sea stars, and between sea stars and other taxa such as crabs (e.g. Menge, 1972; Menge & Menge, 1974; Schmid & Schaerer, 1981; Morissette & Himmelman, 2000; Rogers et al., 2018; St-Pierre et al., 2018).

1.5 Thesis objectives and structure

The present study took advantage of access to well acclimated deep-sea species, i.e. feeding normally and periodically reproducing, as evidenced by past studies from the same laboratory (Mercier & Hamel, 2008; Gale et al., 2013; Montgomery et al., 2017). The three main objectives were to: (1) Identify some of potential food sources of benthic deep-sea taxa, (2) assess their foraging strategies, feeding behaviour, and locomotive behaviour, (3) and identify potential intraspecific and interspecific interactions. These objectives made use of flowing cold-water tank setups and time-lapse video recordings in dark conditions (using infrared lights and cameras) in an attempt to simulate the natural environment and eliminate the potential bias created by bright illumination.

Chapter 2 investigates potential sources of food in the four focal deep-sea species and characterizes their food detection and foraging behaviour in the absence of biotic pressures (singleton trials). Chapter 3 focuses on inter-individual interactions during food acquisition using conspecific and heterospecific mixes (group trials). The latter chapter also examines responses of mesocosm communities to simulated food falls.

By assessing species-specific food preferences and exploring foraging patterns in the absence and presence of competitive pressure from one or more co-existing species under dark laboratory settings, a more comprehensive picture of the behaviour and feeding ecology of a given species can be produced. In addition, preliminary information can be gathered on the overall response of deep-sea taxa to limited food resources. Findings will hopefully provide valuable baseline information for future researchers to use, while also filling a currently missing link between gut content or biochemical analyses of samples and brief/discrete *in situ* observations (under lighted conditions). Exploring feeding strategies in the deep sea should

provide a broader understanding of the intricacies of ecosystem functions and help identify species and habitats that will be most vulnerable to natural or anthropogenic disruptions in food supply, while the study of intra and interspecific competition should help researchers understand which species (or which individuals of a given species) in an ecosystem will be most successful in different settings (e.g. natural vs. disturbed).

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1.7 Figures

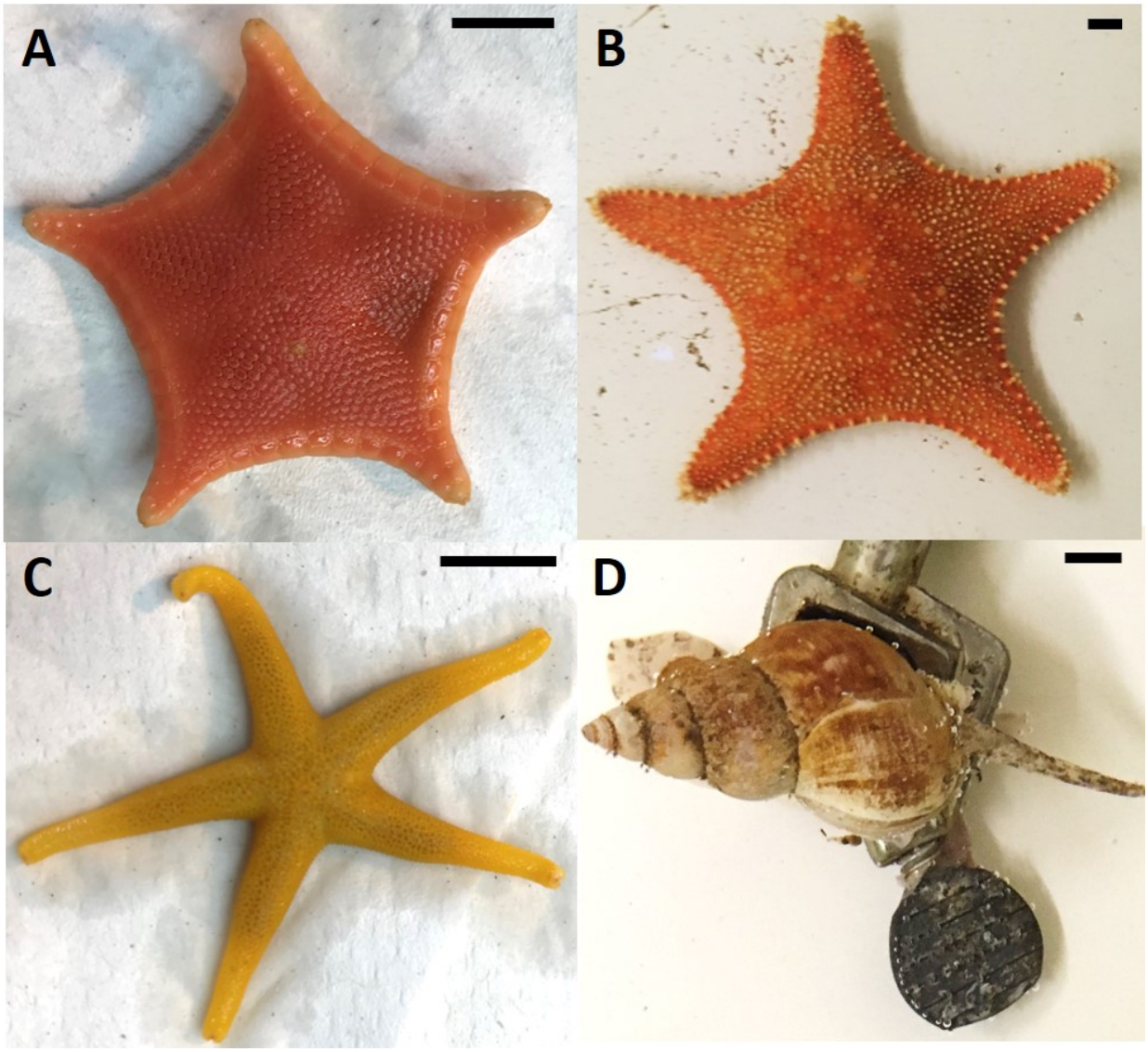

Figure 1.1 Focal species of this thesis: the sea stars (A) *Ceramaster granularis*, (B) *Hippasteria phrygiana*, (C) *Henricia lisa*, and the gastropod (D) *Buccinum scalariforme*. All scale bars represent 1 cm.

Chapter 2 Foraging Strategies and Locomotor Behaviour in Four Deep-Sea Benthic Species*

2.1 Abstract

The feeding behaviour of deep-sea animals is largely understudied despite being of relevance to assess changes in ecosystems functioning in the face of anthropogenic impacts and climate regime shifts. Here, time-lapse videography in dark, cold-water, flow-through laboratory settings were used to study the behaviours of a gastropod (*Buccinum scalariforme*) and three sea stars (*Ceramaster granularis*, *Hippasteria phrygiana*, *Henricia lisa*) from the bathyal Northwest Atlantic, to build knowledge on their foraging strategies (i.e. food search, assessment and handling) and dietary selectivity. In all species tested, the presence/absence of a palatable food source modulated the speed and directionality of movements. Approach trajectories were erratic in the absence of palatable food and targeted in its presence: *C. granularis*, *H. phrygiana*, and *B. scalariforme* moved in straight line to the food, while *H. lisa* moved either in straight line or counterclockwise loop. They approached palatable foods at mean speeds of 0.2, 0.7, 2.9 and 0.6 cm min^{-1}, respectively. At the finer scale, unprecedented pulses in displacement speed were detected, varying in amplitude and frequency depending on the food item. *H. lisa* responded opportunistically to various types of fleshy carrion, suggesting that it may have a broader diet than expected. In contrast, *H. phrygiana* did not accept sea pen carrion (despite being seen to feed on sea pens in the field), although it responded to cup coral carrion. The spongivore and suspected generalist scavenger profile of *C. granularis* was confirmed, while *B. scalariforme* displayed the scavenging lifestyle of buccinids. Based on these results, scavenging may be more widespread in deep-sea gastropods and sea stars than currently assumed from *in situ* observations

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and gut content analysis, likely due to food limitation driving greater flexibility in foraging strategies.

2.2 Introduction

The deep sea is one of the largest environments on Earth (Ramirez-Llodra et al., 2010), and its biota remains largely understudied when compared to more easily accessible continental margin areas (Danovaro et al., 2014). Knowledge of several life traits for the most abundant and prominent deep-sea phyla is being gathered (Bernardino et al., 2012; Drazen & Sutton, 2017). Unfortunately, information on feeding strategies and foraging processes in the food-limited depths of the ocean remains scarce, despite being key life traits and behaviours of relevance for the understanding of ecosystem functioning and productivity (e.g. Yeh & Drazen, 2011; Aguzzi et al., 2018; Danovaro et al., 2020).

The food-web structures of deep-sea benthic ecosystems have been primarily studied by assessing the diet of organisms through stable isotope, fatty acid and gut content analyses (e.g. Amaro et al., 2009; Sahlmann et al., 2011; Würzberg et al., 2011; Gale et al., 2013; Baillon et al., 2014; Drazen & Sutton, 2017; Parzanini et al., 2017; 2018a; 2018b). To date, much of the experimental field and laboratory work regarding feeding and locomotor behaviour in deep-sea taxa centers on crustaceans and fishes (e.g. Klages et al., 2000; Premke et al., 2006; Raymond & Widder, 2007; Braga-Henriques et al., 2011; Sahlmann et al., 2011; Yeh & Drazen, 2011; Doya et al., 2014), while similar knowledge for echinoderms and molluscs is comparatively scant (e.g. Aguzzi et al., 2012).

Contrarily to many shallow-water species of gastropods and sea stars that have been extensively studied under controlled laboratory conditions (e.g. Menge, 1972; Brown & Alexander Jr, 1994; Rochette et al., 1994; Ilano et al., 2005; Lohmann et al., 2016), a limited number of

similar studies have been carried out with deep-sea equivalents (e.g. Hudson et al., 2005; Sahlmann et al., 2011; Gale et al., 2013; Montgomery et al., 2017). Among deep-sea echinoderms, the majority of feeding and behavioural studies have focused on holothuroids (Hudson et al., 2004; Hudson et al., 2005; Amaro et al., 2009), most of which are deposit feeders and nutrient cyclers. Comparatively little exists on other dominant classes (e.g. sea stars, brittle stars) and phyla (e.g. molluscs), which may exhibit a currently undetected diversity of feeding strategies. Gale et al. (2013) conducted laboratory feeding trials along with gut content analysis in the deep-sea sea stars *Hippasteria phrygiana* and *Ceramaster granularis*, showing that the first was predominantly a predator of cnidarians, while the second was a generalist sponge eater with potential scavenging tendencies. *C. granularis* was assumed to also ingest sea pens, based on calcium carbonate sclerites found in its stomach contents (Gale et al., 2013). As for the sea star *Henricia lisa*, it is classified as a sponge eater based on *in situ* observations and laboratory experiments (Mercier & Hamel, 2008; Robertson et al., 2017), but whether it feeds upon other types of prey is uncertain. The diet of shallow-water members of the genus *Buccinum* has been examined (Himmelman & Hamel, 1993; Evans et al., 1996; Ilano et al., 2005), however, nothing specifically addressing the diet of *Buccinum scalariforme* exists, except for a study by Montgomery et al. (2017) who observed this species feeding upon mussel flesh and other carrion in a mesocosm. Work on other deep-sea buccinid gastropods suggest that they can switch from active predation to scavenging strategies depending on the situation, e.g. dead bait or live prey (Aguzzi et al., 2012).

The present work pursued two main objectives: (1) build knowledge on dietary selectivity in benthic deep-sea taxa, and (2) assess their feeding strategies and foraging processes (search, assessment, pursuit and handling of food), including movement paths and speed, and their behaviour when approaching different food sources. This laboratory-based study made use of

access to live specimens of deep-water species, flowing cold-water tank setups and time-lapse video recordings in constant darkness using infrared technologies. Exploring feeding strategies in deep-sea megafauna allows further insight on the functioning of deep benthic ecosystems (*via* feeding strategies), providing relevant data on their vulnerability and resilience in the face of commercial fishing pressure and climate-change alterations of carbon/energy fluxes (Levin & Le Bris, 2015).

2.3 Materials and Methods

2.3.1 Focal Species

The present study focuses on four abundant bathyal species from the Northwest Atlantic: the gastropod *B. scalariforme*, and the sea stars *C. granularis*, *H. phrygiana*, and *H. lisa*. *B. scalariforme* is known to occur down to depths >1100 m in Greenland, Iceland, the Canadian Arctic, Alaska (USA), and both the eastern and western coasts of Canada, and as far south as Maine (USA) (Montgomery et al., 2017). *C. granularis* is found at depths ranging from ~50 to >1400 m in the Canadian Arctic, off Greenland and Iceland, along both coasts of the North Atlantic Ocean, and as far south as the Northeast coast of South America (Gale et al., 2015; Mah, 2019a). *H. phrygiana* is widely distributed throughout the Northern and Southern Atlantic and Pacific oceans as well as in the North Sea, at depths down to 1400 m (Mah et al., 2014) and *H. lisa* is found strictly in deep waters of the North Atlantic basin down to ~1400 m (Mah, 2019b).

2.3.2 Collection and Holding Conditions

All species were collected as trawl by-catch, between 2013 and 2017, during routine multi-species surveys conducted by the Canadian Department of Fisheries and Oceans (DFO) with the CCGS *Teleost* along the coast of eastern Canada between 800-1500 m depths. Collections in late fall and early winter helped ensure that surface temperatures were within tolerable ranges for deep-

sea species (typically ~1-6 °C), minimizing thermal shock during surfacing. Individuals were kept alive onboard in tanks (2000 L capacity) supplied with running seawater pumped from the ocean (~15-20 water change cycles per day). Some other collected species from the deep sea (including Porifera, Cnidaria, and Mollusca) were frozen (-15 to -20°C) to be later used as food items in laboratory trials (see below).

Healthy, undamaged individuals were relocated to the Ocean Sciences Centre of Memorial University (Newfoundland, Canada), where they were housed in 350–800 L tanks, supplied with running (75-250 L h^{-1}) unfiltered seawater at temperatures fluctuating annually between 0-8°C, under atmospheric pressure and constant darkness. Atmospheric pressure was demonstrated to be well tolerated by all species under study, with records of feeding, growth and multiple reproductive events as well as embryonic and larval development (see the results from Mercier & Hamel, 2008; Gale et al., 2013; Montgomery et al., 2017). Holding mesocosms had ~15-20 cm of muddy substrate, available along with some rocks and deep-sea corals. All tested species were housed together with deep-sea corals, except for individuals of *H. phrygiana*, which were kept together in a separate tank to prevent unplanned predation on cnidarians (Gale et al., 2013).

All individuals were acclimated to the laboratory mesocosms for a minimum of a year before using them for experiments and they were determined to be active and in healthy condition, without any visible lesions or injuries (e.g. feeding normally, moving around the tank). Outside of the experimental phase, individuals were fed weekly with flesh from mussels (*Mytilus edulis*), sea urchins (*Strongylocentrotus droebachiensis*), and scallops (*Placopecten magellanicus*), as well as with fresh or thawed sponges, shrimps and other preys collected from the deep sea on an opportunistic basis. These deep-sea preys are similar to those used in experimental trials.

2.3.3 Experimental Conditions

Experiments were conducted between January and June 2018 at atmospheric pressure under total darkness in two 320-L tanks (80 cm wide x 126 cm long x 29 cm deep). The absence of light was determined with a dual-display light meter (VWR International). A LED infrared light (DC 12V) was mounted above each tank along with infrared sensing cameras (Brinno TLC 200 Pro and MAC 200 DN) so that the field of view encompassed the entire tank, similar to Nuñez et al. (2016) and Sbragaglia et al. (2017). Cameras were set to take one picture every 30 seconds; photos were automatically stitched together into a video clip by the integrated camera software. An additional camera (Brinno TLC 200 Pro) was placed at the edge of the experimental tank with a field of view focused on the food item to record finer-scale behavioural interactions. This camera took one picture every 10 seconds to generate a video clip (as above).

Running seawater (31.5 L min^{-1}) was provided through a T-shaped pipe placed 5 cm above the tank bottom with holes drilled along one side every ~2 cm to create a unidirectional uniform and nearly laminar inflow, this was similar to the set up used by Sbragaglia et al. (2015). A similarly shaped drain with holes drilled ~2 cm apart along its surface on all sides was placed at the other end, 25 cm from the tank bottom, to facilitate the outflow. Flow strengths ($\leq$10 cm s^{-1}) were measured across the experimental arena using a handheld flow probe (Hoskin Scientific Flow Meter FP211) and flow directions were measured by injecting ~0.3 mL of food dye at various points near the bottom of the tank (Supplementary Figure S2.1). Experimental tanks had no substrate, as all focal species had been observed to willingly occupy hard substrate surfaces in the holding mesocosm tanks (preliminary observations).

Four replicates of paired experimental and control treatments were run over the course of 2-4 d. In every set of replicates, each tank was used twice for experimental trials and twice for

control trials. The direction of flow was opposite in the two tanks (in both experimental and control conditions) to help control for tank-associated environmental effects. Tanks were emptied of water, scrubbed, and refilled between trials to prevent any buildup of cues from food stimuli or conspecifics. The tanks were filled with ambient seawater and allowed to flow for 10 min before a stimulus (a potential food item or a control; see below) was added. Individuals of all tested species were introduced in the tank 5 min after placement of the stimulus, to allow scent plumes to build up, and were positioned one body/shell length down current from the food (time 0 position, see Supplementary Figure S2.1). Gastropods were placed in the tank with their head facing the current, and sea stars were positioned with the arm closest to the madreporite facing the current, to control for potential leading arm preferences (Montgomery & Palmer, 2012). Individuals were kept submerged and in the dark as much as possible while being transferred between holding mesocosms and experimental setups. No animal was used twice in the span of 48 h.

All species were not fed for two weeks prior to experimental trials, to ensure a similar state of hunger and to mimic sporadic food influx in the deep sea. This period was determined based on previous studies with similar organisms (Rochette et al., 1994; Drolet & Himmelman, 2004; Gale et al., 2013). Sea stars are not negatively impacted by months of starvation (Rochette et al., 1994) and prior studies have determined that some shallow-water gastropods can go 28-42 days without food before significant differences in mortality rates appear between fed and fasted individuals (Lau & Leung, 2004; Tamburi & Martin, 2016).

The experimental trials were run until one of the four predetermined end conditions (adapted from Gale et al., 2013) was met, resulting in trial durations between 6-180 min (depending on the species/food combinations tested). Those conditions were: (1) no movement for 30 min after trial onset (this delay was determined to predict long-term immobility in preliminary trials),

(2) no food approach within 60 min of trial onset, (3) food approach (< 0.5 body lengths away) and then evasion with no second approach within 10 min, and (4) attempt at food consumption. Studies on shallow-water sea stars and gastropods have used similar time frames when studying foraging behaviour (Rochette et al., 1994; Drolet & Himmelman, 2004; Ferner & Weissburg, 2005).

The sizes of all individuals of each species (Table 2.1) were measured while submerged after the completion of each trial, minimizing handling stress. For gastropods, the length of the shell was measured from the apex to the bottom edge of the aperture. Sea star radii were measured using three arms from the center of the disk to the tip of the arm (along the dorsal surface) and used to calculate the diameter.

2.3.4 Food Stimuli

Scavenging and predatory preference experiments tested three main types of food: frozen prey, and either vegetal or detritus pellets (see below). A list of experimental trials per species is available in Table 2.1. The first food category included frozen deep-sea preys: pennatulacean corals (sea pens; *Anthoptilum grandiflorum, Halipteris finmarchica, Pennatula aculeata, P. grandis*), other deep-sea corals (*Duva florida*, *Flabellum alabastrum*), sponges (*Asconema* sp., *Craniella cranium, Geodia* sp., *Iophon* sp., *Mycale lingua, Polymastia grimaldii*), and octopus tentacles (*Graneledone verrucosa*). The soft tissues of the shallow-water blue mussel (*Mytilus edulis*) were also included as prey items. Some of these prey items were chosen based on video surveys conducted by remotely operated vehicles (ROVs), showing their presence in proximity to focal species, as well as from previous diet studies (Gale et al., 2013). All food items were frozen and then thawed at room temperature before being used in the trials. There were also two types of commercial pellets used: Omega One® veggie rounds (mainly composed of kelp and *Spirulina*;

henceforth referred as vegetal pellets), and National Geographic® bottom feeder disks (composed of salmon, kelp, rice bran, wheat flour, shrimp; henceforth referred to as detritus pellets).

For each trial, a pre-weighed amount of food (8-12 g for deep-sea prey, shallow-water mussels, or vegetal and detritus pellets) was always first placed in a precise location in the tank (see above and Supplementary Figure S2.1). Whole cup corals and chunks of soft corals, and sea pens were used, so this weight includes skeletal elements. Regarding pennatulacean coral (sea pen) preys, these were held in a small stainless-steel clamp to keep them upright as per their natural postures in the field. A small, clear plastic pipette was placed upright in a clamp for the control trials against sea pens. All other corals, sponges, and octopus tentacles were placed directly on the bottom of the tank and held by a clamp, or in the case of mussels in a Petri dish to prevent displacement. A small, grey polyresin item (sterile aquarium grade) of similar size was used as a control for the presence of these food items. Both pellet types were of similar size and shape, and they were also placed in a Petri dish (~18-20 pellets per trial weighing ~10 g in total were used). Clear glass aquarium pebbles of similar size and shape to the pellets were used as a control for this food category.

2.3.5 Response Variables and Data Processing

Five categories of behaviour were classified in video analysis: (1) immobile (≤ 1 body length from original location), (2) ignored food (moving around the tank but not distinctly towards the stimulus), (3) close approach of food but no contact (approaches within ≤ 0.5 body length but no contact with stimulus), (4) contact with food (physical contact with stimulus), and (5) accepted food (attempts to feed upon stimulus based upon adoption of feeding postures and/or eversion of the stomach). Each trial was categorized as positive (feeding posture/activity present, i.e. palatable food), negative (food stimulus did not elicit feeding activity/posture such as approaching/touching,

i.e. unpalatable food), and control (inert stimulus). During the recording of experimental trials, the time taken for an individual to reach a food item and assume a feeding posture and/or engage in feeding activity was recorded (or the duration of the trial once an end condition was met, see above).

Locomotor behaviour was analyzed frame by frame over the duration of the trial, using the ImageJ plug-in MtrackJ (Meigering et al., 2012), to determine the following metrics: changes in velocity, mean and maximum displacement speed, total distance traveled, time needed to reach the stimulus (i.e. for positive trials), overall averaged angle of displacement, and the specific path (e.g. animal position relative to the stimulus).

Sea stars were tracked using the middle of the central disk, while the head was used for gastropods (corresponding to oral area in all species). In the event gastropods rolled off the starting zone when initially placed in the tank, due to retreating into their shells, a dashed line was used to represent passive movement in those paths. Locomotor speeds were recorded every 30 s and then averaged into 5 min intervals for the duration that the positive trials ran for each species for determination of general locomotor patterns. Finer scale analysis (speed bursts and their frequency) made use of the 30 s measurements for the entire trial duration length. To calculate average speed at a given time, a minimum of 3 replicate measures for each time point were used for negative and control trials and a minimum of 2 replicates for each time point was used for positive trials (i.e. some species only had 2 positive trials). Angular data were exported from MtrackJ to Oriana v. 4.0 (Kovach Computing Services, Anglesey, Wales), to create circular-linear plots for the angle and speed data. These data were used to determine the mean angle of travel and the resulting mean vector length (denoted as r, ranging from 1 to 0, with values closer to 1 indicating closer clustering around the mean). Food and control items were represented at 180° on

the circle, and speed scales varied between species but were maintained between response types for a given species.

2.3.6 Complementary Trials for Additional Food Stimuli

A set of complementary (not video-based) trials were run in smaller (26 L) tanks, to investigate other food items that observations in the holding mesocosms suggested might be palatable for some of the focal species, but for which time or sample constraints prevented full, experimental replicates. These tanks had a constant supply of ambient unfiltered seawater (~ 25 L h^{-1}) from an inflow that was opposite to the outflow, and they were covered in black material to prevent exposure to light. During these trials, a food item was placed on the bottom of the tank and each individual was added ~5 min later, positioned one body/shell length away from the stimulus. The trial ran for ~24 h, after which the tanks were uncovered for manual inspection of food responses by animals, classified as: (1) active feeding (individuals positioned on the food or actively ingesting it) and/or visible past interaction with food (based on displacement/decrease in weight of food item), or (2) no visible interaction with food item. Between trials, the tanks were cleaned and washed as described earlier.

2.3.7 Data Analysis

Data were analyzed in MaxStat software (V 3.6) to explore the strength of the effect that the response to food (positive, negative, and control trials) had within a species on 5 min binned speed, distance traveled, time between 30 s speed bursts and average amplitude of 30 s speed peaks. Data provided in-text are supplied as mean ± SD where appropriate. One-way analysis of variance (ANOVA) with Bonferroni or Tukey post-hoc tests (for equal or unequal number of observations, respectively) was used if data were normally distributed. Kruskal-Wallis tests with Dunn post-hoc tests were used if data were not normally distributed and/or did not have equal

variances. Overall mean speeds and mean maximum speeds were compared across species using the same tests. A significance threshold of $p < 0.05$ was used for all tests, although data analysis followed the principles of statistical clarity advocated by Dushoff et al. (2019).

2.4 Results

2.4.1 Buccinum scalariforme

Individuals fed upon 4 types of food across all observations (experimental trials and mesocosm feedings, as there were no positive complementary trials): deep-sea octopus, detritus pellets, mussels, and sea urchins (Table S2.1). They fed upon 2 of 7 types of foods that were experimentally tested: octopus (2 of 4 trials) and detritus pellets (1 of 4 trials), but not on deep-sea sponges, deep-sea pennatulacean corals, other deep-sea corals, vegetal pellets, and mussels.

Individuals of *B. scalariforme* approached both palatable food types (octopus and detritus pellets) in experimental settings with the same pattern (Supplementary Figure S2.2, N-P, and Supplementary Video S2.1): firstly (time 0) the siphon displayed sweeping arc motions. Then (between 1-10 min), siphon arc sweeping persisted but was often accompanied with concurrent twisting of the body (including the shell) and little net travel in all trial types (positive, negative, and control). In positive trials (palatable foods), *B. scalariforme* started to move in a relatively straight line towards the food or perpendicular to the current before targeting food with sharp changes in travel angle rather then gradual turns (Figure 2.1A). At this stage, individuals continued siphon sweeping with progressively smaller arcs as they approached the food. Individuals initially reached food using the siphon within 8.9 ± 3.0 min from the start of a trial (first contact time ranged between 7-9 min; Figure 2.2, Supplementary Table S2.1). Siphon touching was followed closely by contact from the head and the leading edge of the foot. Individuals then covered the food item (0.5-2 min after first contact) continuing to sweep their siphon while feeding (Supplementary

Figure S2.3 G, H). Those that fed, moved directly or perpendicularly toward the food before targeting it directly (mean angle of travel across all positive trials 195.5 ± 13.5°, r = 0.97; Figure 2.3A, Supplementary Table S2.1), compared to negative and control trials, where there were no directional trends (91.5 ± 114.5°, r = 0.14 and 131.5 ± 82.9°, r = 0.35, respectively; Figure 2.3B, C, Supplementary Table S2.1). When approaching octopus the average speed was 1.6 ± 0.8 cm min^{-1} and when approaching detritus pellets the average speed was 4.1 ± 1.4 cm min^{-1} (Figure 2.4A), while in negative and control trials the mean speeds were 3.2 ± 2.8 cm min^{-1} and 2.2 ± 2.0 cm min^{-1}, respectively (Figure 4A). However, the nature of the response clearly affected distance traveled; individuals approaching food sources in positive trials traveled less than individuals in negative trials ($F_{3,49} = 3.064$, $p = 0.037$; Figure 2.5) but no other clear differences were determined. Individuals approaching octopus tentacle moved a total of 15.6 ± 11.8 cm over a time of 6.8 ± 3.8 min while the single individual that approached the detritus pellets moved 44.6 cm in 11 min. Individuals in negative and control trials by comparison moved 132.7 ± 40.0 cm and 114.6 ± 42.1 cm, respectively over the course of ~60 min (Figure 2.5). When all trials (regardless of response type) were pooled together, the effect of focal species was clear on all speed metrics. *B. scalariforme* had greater mean speed (2.9 ± 0.8 cm min^{-1} or 0.4 ± 0.1 body lengths min^{-1}; $F_{3,105} = 59.504$, $p < 0.0001$) and maximum speed (9.5 ± 2.7 cm min^{-1} or 1.4 ± 0.4 body lengths min^{-1}; $F_{3,105} = 64.368$, $p < 0.0001$) than all other species in the study (Figure 2.6, Supplementary Table S2.1).

Overall, during experimental trials *B. scalariforme* displayed a high level of activity (remaining immobile in only 2% of trials; Figure 2.7) and often spent their time exploring the tank (ignoring food/stimulus in 82%; Figure 2.7). Detailed examination of movements showed that instead of a constant speed over time, individuals displayed pulses of speed. The average period between peak speeds was not clearly different among responses, i.e. 1.75 ± 0.7 min, 1.6 ± 0.7 min,

and 1.5 ± 0.5 min for positive, negative and control trials, respectively (H_2 = 1.137, p = 0.566; Figure 2.8A, Supplementary Table S2.1). However, the greatest amplitude in a period occurred in positive trials (2.7 cm min^{-1}) while negative (1.3 cm min^{-1}) and control (1.4 cm min^{-1}) trials had similar low-high speed amplitude maxima (Figure 2.8A, Supplementary Table S2.1). The average amplitude was clearly higher in positive trials (1.88 ± 0.81 cm min^{-1}) than in negative (0.67 ± 0.29 cm min^{-1}) or control trials (0.57 ± 0.30 cm min^{-1}; $F_{2,77}$ = 33.231, p <0.0001; Supplementary Table S2.1).

2.4.2 Ceramaster granularis

This sea star fed upon 7 types of food across all observations (experimental trials, complementary trials, and mesocosm observations): deep-sea sponge, deep-sea octopus, detritus pellets, mussel, sea urchin, scallop, and deep-sea gastropod (Table 2.1). Out of six food types tested in experimental trials (deep-sea sponges, deep-sea pennatulacean corals, other deep-sea corals, vegetal pellets, detritus pellets, and octopus), it fed on octopus (2 of 4 trials) and deep-sea sponge (i.e. *Mycale lingua*; 1 of 4 of trials, Table 2.1).

Palatable food items in experimental trials were approached essentially the same way (Supplementary Figure S2.2 A-C): firstly (time 0), the podia located at the tips of the five arms fully extended and moved in lateral sweeping motions with the ocelli at the tips of the arms exposed. This was true for all trials where individuals moved, regardless of responses. Individuals started to approach the stimulus after ~5 min of immobility, with the arm closest to the food leading (i.e. the closest to the madreporite; see section 2.3.3). *C. granularis* traveled in relatively straight lines while approaching food items (Figure 2.1B). Contact with food was initially made with the podia and tip of the leading arm (time 30-32 min; Figure 2.2). Within 1-3 min after initial contact, individuals moved onto the food until most of the body surface was resting on it, and then assumed

a ‘bell’ posture over it (time 31-35 min; Supplementary Figure S2.2 D). When feeding, undulation of the dorsal body wall was visible, and the stomach was everted on the prey. *C. granularis* reached food in 34.8 ± 0.5 min with similar means for both octopus and sponge food types (i.e. positive trials, Figure 2.2, Supplementary Table S2.1). When individuals attempted to feed, they favoured moving in the direction of the food stimulus (180°), traveling at an average angle of 173.4 ± 11.9° (r = 0.98; Figure 2.3D, Supplementary Table S2.1), while in negative and control trials the movement was erratic (21.4 ± 87.0°, r = 0.32 and 336.4 ± 106.9°, r = 0.18, respectively; Figure 2.3E, F, Supplementary Table S2.1). There were no clear differences in the mean travel speed between different responses; both types of positive foods resulted in travel speeds of 0.2 ± 0.1 cm min^{-1} (Figure 2.4B, Supplementary Table S2.1), while negative and control trials both resulted in travel speeds of 0.1 ± 0.1 cm min^{-1} (Figure 2.4B, Supplementary Table S2.1). Likewise, there were no clear differences in the distance traveled between response types ($F_{3,9}$ = 1.747, p = 0.227) although positive trials involving octopus resulted in the shortest travel distance (6.7 ± 0.4 cm) followed by the positive trial involving the deep-sea sponge *M. lingua* (9.0 cm; Figure 2.5). Individuals in control trials travelled a distance similar to individuals responding to *M. lingua* (10.4 ± 4.7 cm), while those in negative trials traveled more (19.4 ± 7.4 cm; Figure 2.5). Across all responses, *C. granularis* traveled at a speed of 0.2 ± 0.1 cm min^{-1} (0.05 ± 0.01 body lengths min^{-1}) and displayed a maximum speed of 1.0 ± 0.2 cm min^{-1} (0.2 ± 0.1 body lengths min^{-1}; Figure 2.6, Supplementary Table S2.1).

Overall, during experimental trials, *C. granularis* displayed a high rate of immobility, with individuals falling into this behaviour category in 73% of trials. Rates of immobility were higher in negative (88%) and control trials (79%) than during replicates of trials where individuals responded to food at least once (25%), even if actual feeding was only ascribed to 38% of the latter

trials (Figure 2.7A-C). Closer examination of movement patterns showed that individuals exhibited distinct pulses of speed (Figure 2.8B). The average period between peak speeds was not clearly different across responses (positive, negative, and control), which showed similar averages, i.e. 1.6 ± 0.7 min, 1.5 ± 0.6 min, and 1.6 ± 0.5 min, respectively ($F_{2,89} = 0.261$, $p = 0.771$; Figure 2.8B, Supplementary Table S2.1). The maximum amplitude between minimum and maximum speed was found in positive trials (0.33 cm min^{-1}), followed by negative trials (0.29 cm min^{-1}) and control trials (0.24 cm min^{-1}; Figure 2.8B, Supplementary Table S2.1). The average amplitude was clearly lower for controls (0.07 ± 0.05 cm min^{-1}) than for positive (0.20 ± 0.07 cm min^{-1}) or negative responses (0.10 ± 0.12 cm min-^{1}; $H_2 = 33.544$, $p < 0.0001$; Supplementary Table S2.1).

2.4.3 Hippasteria phrygiana

This sea star was confirmed to feed upon 6 types of food across all observations (experimental trials, complementary trials, and mesocosm observations): the cup coral *F. alabastrum*, vegetal pellets, gastropod tissue (unidentified deep-sea species), mussels, sea urchins, and scallops (Table 2.1). Out of the six food types tested experimentally in trials (deep-sea sponges, deep-sea pennatulacean corals, other deep-sea corals, vegetal pellets, detritus pellets, and octopus), *H. phrygiana* fed upon cup coral (1 of 4 trials) and vegetal pellets (1 of 4 trials, Table 2.1).

The foraging of *H. phrygiana* towards palatable food items varied in some respects; however, it involved a relatively straight path in both positive trials (Figure 2.1C). In all trials, this species traveled with the tips of its arms curled up, exposing the terminal ocelli, and extending and sweeping the podia located at the tips of the arms. In the presence of vegetal pellets (Supplementary Figure S2.2 D-F, Supplementary Video S2.2) individuals began to move towards the food with the arm closest to the pellets leading (time 10 min; see section 2.3.3). Initial contact with the pellets was made with the podia located at the tip of the leading arm (time 81 min; Figure

2.2, Figure 2.4 C, Supplementary Figure S2.2 H). Thereafter, *H. phrygiana* moved over the pellets until it covered them entirely and everted its stomach (time 105 min; Supplementary Figure S2.2 I, S2.3 I). The main difference in the foraging process in the presence of the cup coral *F. alabastrum* (Supplementary Figure S2.2 J-M) was that, after initial contact with the coral (time 21 min; Figure 2.2, S2.2 K), the leading arm steadily made fuller contact with the coral and began to pull it towards the mouth (time 21-24 min; Supplementary Figure S2.3 L). Once the coral was beneath their mouth, a feeding 'bell' posture was assumed with each of the arms making partial contact with the bottom of the tank (time 25 min; Supplementary Figure S2.2 M). Sweeping podia movement was still visible at the tips of the arms once the individual began to feed. Final feeding posture can be seen in Supplementary Figures S2.2 M, S2.3 E, and Supplementary Video S2.3. *H. phrygiana* had a highly variable response time, taking longer to react to vegetal pellets (~80 min) than to cup coral (~21 min; Figure 2.2, Supplementary Table S2.1). Individuals attempting to feed distinctly took a more direct path toward the position (180°) of the food (172.8 ± 9.0°, r = 0.99; Figure 2.3G, Supplementary Table S2.1), whereas individuals in negative and control trials showed haphazard direction of travel (7.4 ± 121.7°, r = 0.11, and 353.0 ± 110.5°, r = 0.16 respectively; Figure 2.3H, I, Supplementary Table S2.1). *H. phrygiana* moved more quickly when attempting to feed upon cup coral (0.9 ± 0.5 cm min^{-1}) than in any of the other trials (Figure 2.4C). Conversely, *H. phrygiana* moved slower when attempting to feed on the vegetal pellets (0.2 ± 0.1 cm min^{-1}) than in negative trials (0.5 ± 0.3 cm min^{-1}), while they moved at a similar speed in negative trials and control trials (0.4 ± 0.2 cm min^{-1}; Figure 2.4C). Despite the differences detected in speed during some trials, responses did not have a clear effect on total distance traveled by individuals ($F_{3,19}$ = 0.645, p = 0.596; Figure 5). Overall, across all trials, *H. phrygiana* traveled at

a speed of 0.7 ± 0.4 cm min^{-1} (< 0.1 body length min^{-1}) and had a maximum speed of 2.6 ± 1.2 cm min^{-1} (0.2 ± 0.1 body lengths min^{-1}; Figure 2.6, Supplementary Table S2.1).

During experimental trials, *H. phrygiana* remained immobile in about half of the trials (Figure 2.7). A notable proportion of individuals displayed no/minimal movement across positive trial replicates (63%), and negative (50%) and control (46%) trials (Figure 2.7A-C). *H. phrygiana* also had a low rate of food acceptance when presented with foods determined to be palatable to the species (25%; Figure 2.7A). Examination of the movement patterns on a finer scale showed that individuals displayed locomotor pulses rather than traveling at consistent speeds throughout the trials (Figure 2.8C). The period between speed peaks was 1.6 ± 0.7 min for positive trials, 1.5 ± 0.6 min for negative trials, and 1.5 ± 0.5 min for control trials, with no statistically clear differences (H_2 = 0.435, p = 0.805; Supplementary Table S2.1). The largest amplitude between minimum and maximum speed occurred in positive trials (1.4 cm min^{-1}), while amplitude was smaller in negative (0.9 cm min^{-1}) and control trials (0.4 cm min^{-1}; Figure 2.8C, Supplementary Table S2.1). The average amplitude was clearly lower in controls (0.17 ± 0.12 cm min^{-1}) than in positive (0.47 ± 0.37 cm min^{-1}) or negative trials (0.18 ± 0.15 cm min^{-1}; H_2 = 17.058, p = 0.0002; Supplementary Table S2.1), while there was no clear difference detected between positive and negative responses.

2.4.4 Henricia lisa

This sea star fed upon 7 types of food across all observations (experimental trials, complementary trials, and mesocosm observations): deep-sea sponges, detritus pellets, mussels, urchins, scallops, octopus tentacle, and unidentified deep-sea gastropod tissue (Table 2.1). Out of 3 types of food that were tested experimentally (deep-sea sponges, detritus pellets, and vegetal pellets) *H. lisa* only fed upon deep-sea sponges (4 of 4 trials; Table 2.1).

Even though the species of deep-sea sponge differed across the replicate experimental trials (3 species in total: *Mycale lingua*, *Geodia* sp., and *Iophon* sp.), *H. lisa* approached palatable food consistently (Supplementary Figure S2.2 N-P). At the onset (time 0 min) the arm closest to the food (original orientation, see section 2.3.3) began to stretch out in the direction of the food before the other arms or main body began to move (time 5-10 min), except for one trial where the individual followed an arc and then approached the food using an arm other than the one initially placed closest to the food. Half of the individuals responding to food followed a straight line, the other half followed a loop, initially moving in a downstream direction and counter-clockwise, before moving toward the food (Figure 2.1D). Initial contact with the various sponges was made with the tip of the leading arm (two arms side-by-side in one case) at time 26, 72, or 77 min depending on the trial (Figures 2.2, 2.4D). Afterwards the individual reached up to make fuller contact with the leading arm(s) and, soon after (within 3-4 min), with the remaining arms (time 30, 75-78 min, depending on the trial). The individual then crawled up onto the sponge, wrapped its arms around it and began to feed by evaginating its stomach, conforming its body closely to the curves of the sponge (times 30, 80-85 min). An example of the final feeding posture is seen in Supplementary Video S4. *H. lisa* had a slow reaction time to food cues on average, taking ≥70 min to make initial contact with food in 3 of 4 trials, regardless of the species of sponge used. Despite equal use of direct or looped paths, the average angle of travel in positive trials still favoured the direction of food (175.4 ± 27.8°, r = 0.89; Figure 2.3 J, Supplementary Table S2.1), while travel direction in negative and control trials was haphazard (43.6 ± 75.5°, r = 0.42, and 345.0 ± 106.8°, r = 0.18 respectively; Figure 2.3K, L, Supplementary Table S2.1). Mean speeds were as follows: *Iophon* sp. (0.1 ± 0.2 cm min^{-1}), *M. lingua* (0.5 ± 0.2 cm min^{-1}), *Geodia* sp. (0.6 ± 0.4 cm min^{-1}), negative trials (0.7 ± 0.2 cm min^{-1}), and control trials (0.5 ± 0.2 cm min^{-1}, Figure 2.4 D). There

were no statistically clear differences in the distance traveled across positive food types or negative and control responses ($F_{4,16} = 0.491$, $p = 0.743$; Figure 2.5). Overall, across all trials, *H. lisa* moved at a speed of 0.6 ± 0.1 cm min^{-1} (0.11 ± 0.03 body lengths min^{-1}) and displayed a maximum speed of 2.0 ± 0.3 cm min^{-1} (0.39 ± 0.06 body lengths min^{-1}; Figure 2.6, Supplementary Table S2.1).

During experimental trials, *H. lisa* nearly always moved around regardless of response type; it remained immobile in only 4% of trials and exclusively in the absence of food (8% of control trials, Figure 2.7C). *H. lisa* had a high rate of food acceptance in this study (100%) when presented with food items that experimental trials determined were palatable for the species (Figure 2.7A). Closer examination of the movement of individuals during trials revealed similar pulse speed patterns as in the other focal species (Figure 2.8D). The average period between peaks in speed for the different responses were 1.44 ± 0.42 min, 1.52 ± 0.48 min, and 1.57 ± 0.63 min for positive, negative and control trials, respectively, with no statistically clear effects detected ($H_2 = 0.543$, $p = 0.762$; Figure 2.8D, Supplementary Table S2.1). The greatest amplitude was seen in the positive trials (1.02 cm min^{-1}), followed by negative trials (0.97 cm min^{-1}) and control trials (0.43 cm min^{-1}; Figure 2.8D, Supplementary Table S2.1). The average amplitude was clearly lower in control trials (0.20 ± 0.12 cm min^{-1}) than when there was a positive (0.31 ± 0.17 cm min^{-1}) or negative (0.33 ± 0.21 cm min^{-1}) response to food ($H_2 = 8.396$, $p = 0.015$; Supplementary Table S2.1).

2.5 Discussion

Finding and successfully consuming food is among the most fundamental activities of all living organisms (Lohmann et al., 2016; Liu et al., 2019). Results of the present study showed that the gastropod *B. scalariforme* and the sea star *H. phrygiana*, two eurybathic species, responded to 50% and 60% of foods offered across all observations, respectively; whereas the sea stars *C.*

granularis and *H. lisa*, which are restricted to deeper waters, responded to 70% and 88% of foods offered across all observations, respectively. These data suggest that strict deep-sea species could be less selective and favour more opportunistic diets than eurybathic or shallow-water counterparts. Scavenging behaviours prevailed in all tested species, even those that were previously believed to have been specialized predators (i.e. spongivores). Increased scavenging in deep-sea megabenthic species is likely a depth-related life trait (Yeh & Drazen, 2011), which can be attributed to a decrease in nutrient resources across depths (Childress, 1995; Premke et al., 2006; Higgs et al., 2014).

When exposed to a palatable food source, all tested species showed differing mean response times. Among the sea stars, *C. granularis* had the fastest mean response, *H. lisa* had the slowest, while *H. phrygiana* had variable intermediate responses. *H. lisa* only fed upon sponges in the experimental trials, which are sessile and often large, thus able to accommodate several individuals at once (Mercier & Hamel, 2008; Robertson et al., 2017). Reduced competition for this resource could explain the slow response times of *H. lisa*. *H. phrygiana* responded to and reached the cup coral faster among all palatable food items provided, similar to how this species reached cup corals faster than other food in the study performed by Gale et al. (2013). This may represent a competitive response, as cup corals are small in comparison to *H. phrygiana* and are likely monopolized by a single individual. *C. granularis* displayed the fastest and most consistent response time among the sea stars, regardless of the food offered, even though it was the slowest species, highlighting its opportunistic diet (Gale et al., 2013). Conversely, the gastropod *B. scalariforme* showed the fastest response globally, maybe due to its higher movement speed capacity.

The movement patterns used to approach food items provide further insight on the feeding ecology of tested species. *B. scalariforme*, *C. granularis*, and *H. phrygiana* took relatively direct routes to their food, while *H. lisa* took either a direct route or a counterclockwise loop which crossed the dominant current. Cross-current foraging movements have been identified in some shallow-water sea stars, possibly to enable individuals to assess chemical cues over a wider spatial range (e.g. Rochette et al., 1994; Drolet & Himmelman, 2004); however, looping paths were never described before to our knowledge. *H. lisa* may use this strategy to scan its surroundings (e.g. for the presence of predators), before engaging in feeding activity. The behaviour does not appear to be related to the type of prey (e.g. *Geodia* sp. was approached with both a straight path and a looping path).

The sea stars in this study were always initially oriented with the arm closest to the madreporite pointing towards the stimulus. In the presence of palatable food, they always kept this arm facing forward as they closed in on the stimulus. However, in the absence of palatable food, individuals changed direction without rotating the body to maintain a specific leading arm. The present results thus suggest that any arm exposed to the strongest cue becomes the leading arm in these three sea star species, in line with a previous study on chemosensory search behaviour in the sea star *A. forbesi* (Dale, 1999).

Analysis of speed patterns provided insight into the potential effects of different food stimuli (i.e. attraction or repulsion) on the tested species. Surprisingly, individuals were not always moving fastest when exposed to palatable food items, as initially hypothesized. For example, *B. scalariforme* moved the fastest in the presence of unpalatable food like corals and sponges, likely due to the presence of chemical deterrents (Takai et al., 1987; Karthikayalu et al., 2010). In contrast, *H. lisa* was attracted by sponges but with inconsistently higher or lower movement speeds

than when exposed to unpalatable and control stimuli. Differential approaching speeds were seen by this species toward the sponges *Iophon* sp. (slower) and *Geodia* sp. (faster), suggesting different levels of attraction and hence preference. *H. lisa* traveled quickly in the presence of, and often away from, unpalatable food, further supporting the potentially repulsive nature of some corals (as for *B. scalariforme*). *H. phrygiana*, by comparison, traveled at similar speeds when exposed to unpalatable and control stimuli; however, exposure to some palatable food items (e.g. cup corals) resulted in higher speeds, whereas other palatable foods resulted in lower speeds (e.g. vegetal pellets). Out of the four focal species, only *C. granularis* consistently traveled more quickly toward palatable than unpalatable food items or controls. This suggests that this species may not be repulsed by the chemical signatures of unpalatable food types such as corals, although individuals were previously seen to turn away from living corals after initial physical contact (presumably to avoid defensive nematocysts; Gale et al., 2013). The slower speeds seen in some species (*B. scalariforme*, *H. lisa*, *H. phrygiana*) when approaching some palatable food items could also be a trade-off between travel speed and sensory awareness of the surroundings. Dale (1997) found that when the sea star *A. forbesi* was approaching food, it moved more slowly than individuals that were in control trials or those that did not approach food, suggesting that slower movement may enable some sea stars to more accurately assess chemical signatures to locate food.

All focal species exhibited speed modulation pulses (bursts), with a period and amplitude that varied based upon the nature of the stimulus. The average time taken to complete a step (i.e. the period) did not consistently relate to the palatability of the food across species. *B. scalariforme* exhibited longer periods between peak speeds when exposed to palatable food, while *H. lisa* displayed the shortest mean periods in similar situations, with *C. granularis* and *H. phrygiana* falling in between. However, the difference between the maximal and minimal speed reached

during a period (i.e. the amplitude) was always greatest in response to palatable stimuli rather than unpalatable stimuli or controls. This suggests finer adjustment of speed in trials with palatable food. As speed bursts were detected in members of two phyla (echinoderms and molluscs), it may be a common locomotor pattern to several vagile benthic marine animals, although such behaviour has never been reported before, to our knowledge. In locomotor studies, individuals are generally described as moving at more constant speeds (e.g. Rochette et al., 1994; Kidawa et al., 2010; Montgomery & Palmer, 2012; Hemmert & Baltzley, 2016; Lohmann et al., 2016). Perhaps this is because of the nature of the stimulus used in other investigations; e.g. escape responses (Montgomery & Palmer, 2012) are likely to trigger sustained maximum speed. It could also be a question of temporal scale. Here, this phenomenon was revealed by fine-scale analysis (every 30 s). In other studies, either a single mean speed value was provided for the entire trial without mention of fine-scale measurements (Kidawa et al., 2010; Hemmert & Baltzley, 2016), or frames were analysed every 200-300 s (Rochette et al., 1994; Lohmann et al., 2016). The mechanism behind the pulsing movement speed patterns remain unclear; it may be associated with foot undulation periods in gastropods or podia coordination in sea stars resulting in 'steps' (e.g. full undulation of the muscular foot or time required for griping and pulling action of podia).

A corollary benefit of the present study was to confirm, challenge or extend the known diets of focal species. According to Gale et al. (2013), *H. phrygiana* can feed upon various species of live soft corals and sponges in the laboratory. Here, it did not feed upon the thawed sea pens, octocorals, or sponges, suggesting a preference for those prey to be alive; however, it did feed upon thawed cup coral and vegetal detritus pellets, highlighting a prey-specific scavenging response. *H. phrygiana* typically curled the tips of its arms 90° to expose its ocelli during the trials, hinting at possible visual assessment of its surroundings (Birk et al., 2018), possibly in search of

bioluminescent signals produced by some deep-sea species, including sea pens and other corals (Weightman & Arsenault, 2002; Smith et al., 2017). The use of dead (non-bioluminescent) sea pens could explain the disinterest towards those prey types exhibited in the present study.

Here, *C. granularis* preyed upon various species of sponges as well as on tentacles of deep-sea octopus in live trials, but curiously not on sea pens. The latter is perhaps not an acceptable carrion food source as discussed in *H. phrygiana* (see above). Gale et al. (2013) found sclerites from sea pens, siliceous sponge spicules, and benthic foraminiferans in the gut contents of wild-caught *C. granularis*, whereas individuals used in their laboratory trials preyed upon sponges. The different results obtained here suggest that all carrion is not equally palatable in laboratory trials, for reasons that have to be yet determined.

H. lisa in the present study fed upon a variety of fleshy foods, challenging the notion that it is strictly spongivorous (Mercier & Hamel, 2008; Robertson et al., 2017) like other members of this genus (Sheild & Witman, 1993). In fact, *H. lisa* presented one of the most generalist diets in comparison to the other tested species and had the highest overall rate of food acceptance. Perhaps the scavenging tendencies of *H. lisa* and *C. granularis* have been under-reported because food falls are rarely observed *in situ* (Klages et al., 2000; Premke et al., 2006; Higgs et al., 2014) and many types of foods lack the small hard parts that would linger in the stomach of these animals long enough to be detected in gut-content analysis (contrary to spicules of sponges or sclerites of corals). Combined spongivory and carrion feeding in *H. lisa* may be an advantage when considering its dual brooding and broadcasting spawning strategy (Mercier & Hamel, 2008). Juveniles that have been brooded are probably more likely to be released close to the feeding grounds of adults (e.g. sponge gardens), while propagules that were broadcasted may settle far

from these habitats. The ability to feed opportunistically on carrion would likely increase their survival potential.

Unsurprisingly, the gastropod *B. scalariforme* displayed broad scavenging, feeding upon deep-sea octopus and detritus pellets, in line with the opportunistic behaviour typical of buccinids (Evans et al., 1996; Ilano et al., 2005; Aguzzi et al., 2012). However, when compared to data from shallow-water members of the same genus (e.g. Evans et al., 1996; Ilano et al., 2005), *B. scalariforme* responded faster to food sources. A scarcity of food in the natural environment of *B. scalariforme* (Premke et al., 2006; Higgs et al., 2014; Smith et al., 2015) may drive individuals to respond more efficiently to palatable cues.

This study provides new data on the behaviour of abundant deep-sea megafauna, shedding new light on the processes of detection, assessment, and handling of food. Results indicate that reliance on scavenging may be more widespread in deep-sea gastropods and sea stars than previously inferred from *in situ* observations or gut content analysis. The food-limited environment may drive greater flexibility in foraging strategies for given taxa living in the deep sea, compared to related species living in shallow-water environments. In addition, species-specific responses were detected in terms of locomotor speed and trajectory toward palatable food items, suggesting that some species may be trading speed for sensory awareness and detection. Finally, the unprecedented locomotor speed pulses noted at fine temporal scales in the focal species, which belong to two phyla, warrant further study in deep-water and shallow-water benthic taxa. Overall, life traits in deep-sea species are not yet well understood, calling for more studies on their foraging strategies to help build our understanding of their potential functions within ecosystems. In turn, such knowledge can inform us of their putative vulnerabilities to ecological disturbances, including

cascading changes in prey availabilities, and provide an overall more complete picture of the structure and dynamics of deep-sea food webs.

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2.7 References

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2.8 Tables and Figures

Table 2.1 List of experimental trials and feeding responses. Bolded food types indicate foods used in experimental trials for that species (4 replicates).

Species (n = number of individuals)	**Average shell length/radius (cm, Mean ± SD)**	**Food Type**	**Response**
Buccinum scalariforme	6.8 ± 0.7	**Sponges**	0 positive trials
		Pennatulacean Corals	0 positive trials
(n = 6)		**Other Corals**	0 positive trials
		Detritus Pellets	1 positive trial
		Vegetal Pellets	0 positive trials
		Octopus	2 positive trials
		Mussels	0 positive trials*
		Sea Urchins	No trials*
Ceramaster granularis	2.3 ± 0.6	**Sponges**	1 positive trial
		Pennatulacean Corals	0 positive trials
(n = 16)		**Other Corals**	0 positive trials
		Detritus Pellets	0 positive trials*
		Vegetal Pellets	0 positive trials
		Octopus	2 positive trials
		Mussels	No trials*
		Sea Urchins	No trails*
		Scallops	No trials*
		Gastropods	No trials*/**
Hippasteria phrygiana	7.7 ± 1.2	**Sponges**	0 positive trials
		Pennatulacean Corals	0 positive trials
(n = 14)		**Other Corals**	1 positive trial
		Detritus Pellets	0 positive trials
		Vegetal Pellets	1 positive trial
		Octopus	0 positive trials
		Mussels	No trials*
		Sea Urchins	No trials*
		Scallops	No trails*
		Gastropods	No trials**
Henricia lisa	2.7 ± 0.5	**Sponges**	4 positive trials
		Detritus Pellets	0 positive trials*
(n = 8)		**Vegetal Pellets**	0 positive trials
		Octopus	No trials*/**
		Mussels	No trials*
		Sea Urchins	No trials*
		Scallops	No trials*
		Gastropods	No trials*/**

*Observation of feeding in holding mesocosm

**Observation of feeding in complementary experiments

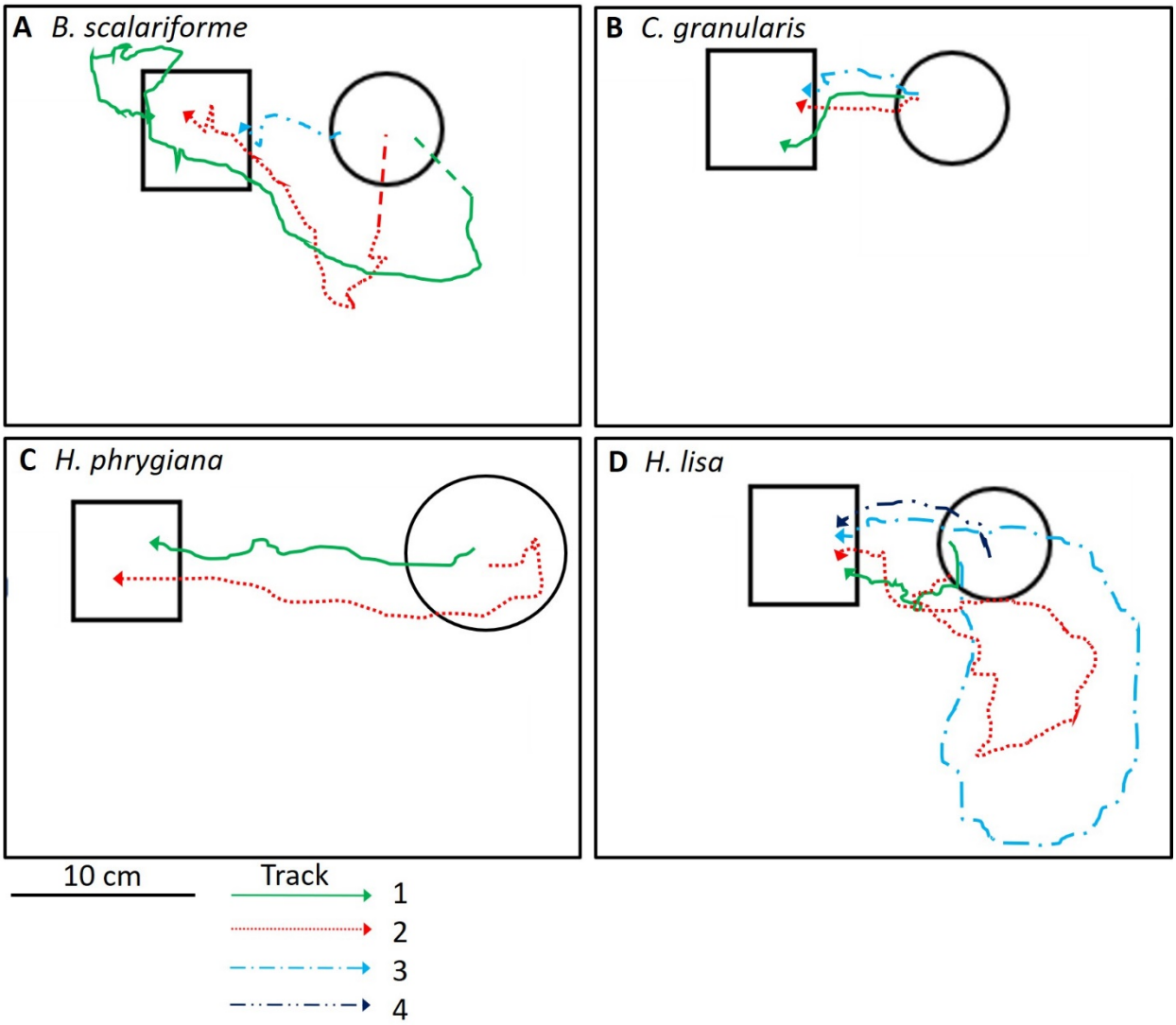

Figure 2.1 Paths taken by (A) *B. scalariforme*, (B) *C. granularis*, (C) *H. phrygiana*, (D) *H. lisa* when approaching positive food items. The circle represents the starting position (location and size adjusted for size of species) and the square represents the food (placed ~1 body length up current from experimental individual). The bar in the legend represents a distance of 10 cm and each panel represents an area that's approximately 875 cm^2. Dashed lines in panel A represent where individuals passively rolled off the starting zone prior to actively moving (because they had withdrawn into their shells while being placed in the tank). Curved section of path in track 1 of panel B is due to the individual moving along the edge of the food before starting to feed. For details on tank and current vectors see Supplementary Figure S2.1.

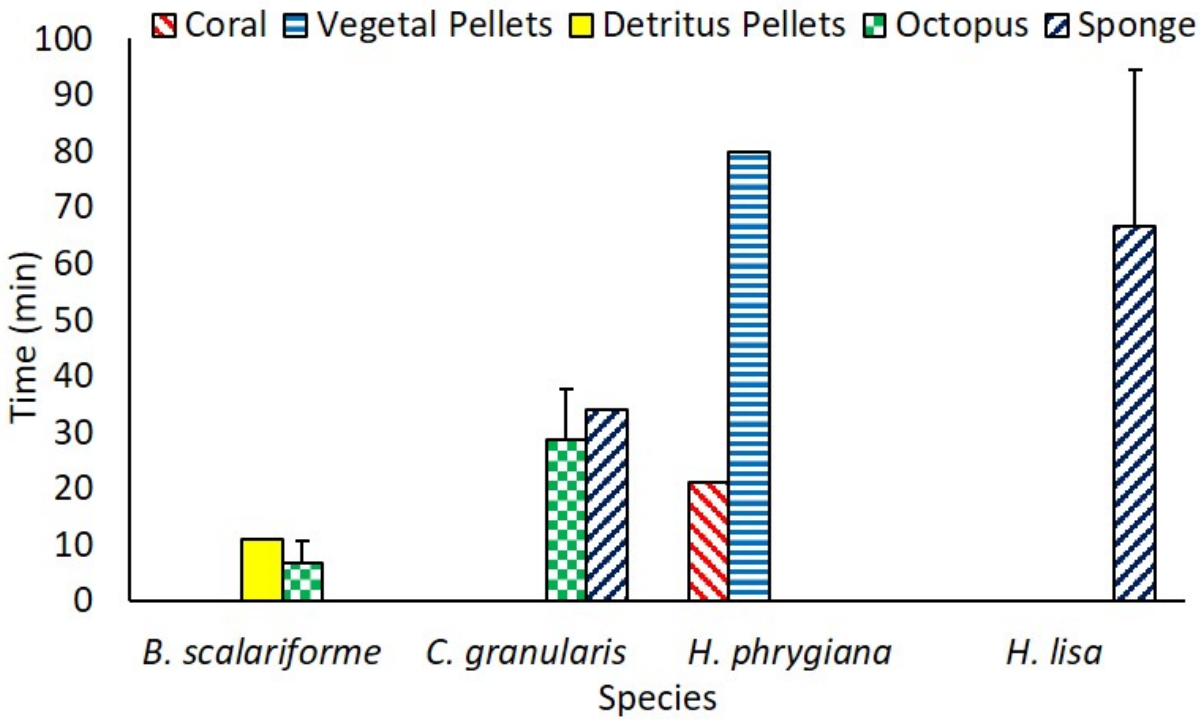

Figure 2.2 Mean time in minutes (± SD, where applicable) until initial contact with positive food types for each focal species during experimental trials. Coral refers to non-pennatulacean/other corals (see Table 2.1). All sponge species were pooled for *H. lisa*.

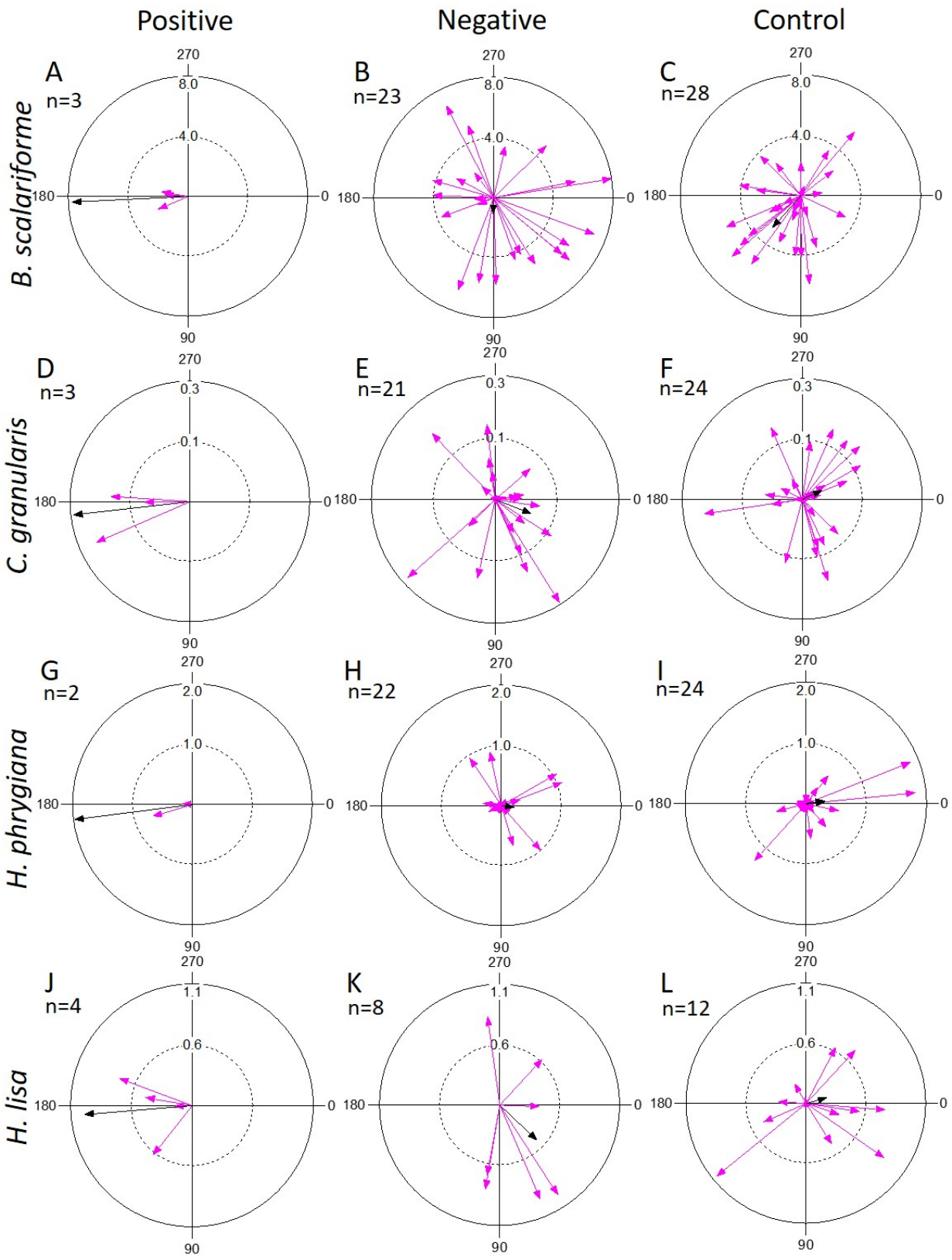
Positive
Negative
Control
B. scalariforme
C. granularis
H. phrygiana
H. lisa
A
n=3
B
n=23
C
n=28
D
n=3
E
n=21
F
n=24
G
n=2
H
n=22
I
n=24
J
n=4
K
n=8
L
n=12
270
90
180
0
8.0
4.0
0.3
0.1
2.0
1.0
1.1
0.6

Figure 2.3 (previous page) Circular plots illustrating average path direction (vectors) taken by *B. scalariforme* (A-C; two negative trials removed due to video issues), *C. granularis* (D-F), *H. phrygiana* (G-I) and *H. lisa* (J-L). Food items were placed in the 180° direction (left). Pink arrows represent individual trial vectors while the black arrow is the mean vector (r) for the number (n) of trials (with a value of 1 being assigned to the outer circle for this vector in all cases). Movement speed (values within the circle) is expressed in cm min^{-1}. Note that scales (intervals expressed by concentric circles) vary between species.

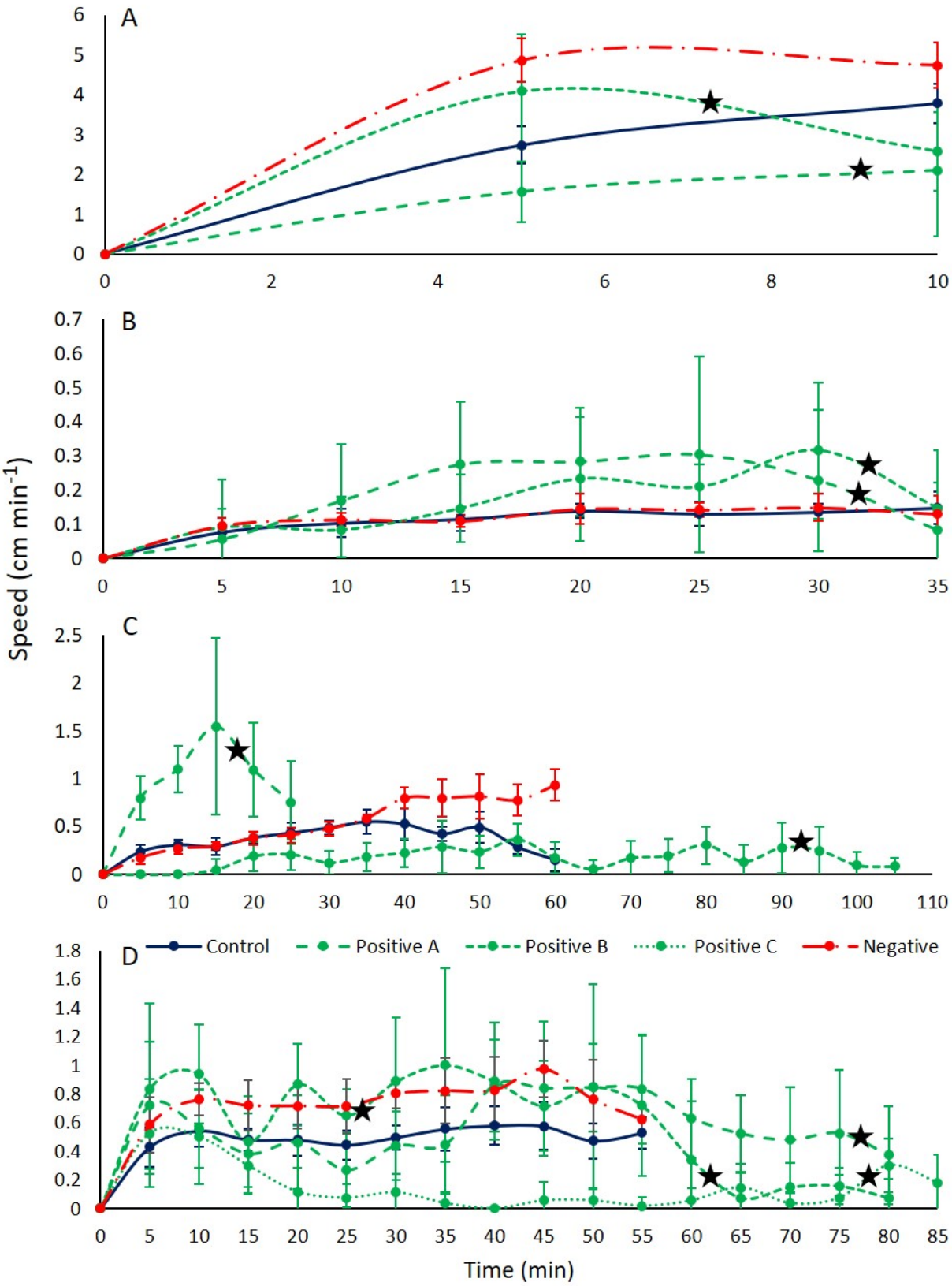
A
B
C
D
Speed (cm min-1)
Time (min)
Control
Positive A
Positive B
Positive C
Negative

Figure 2.4 (previous page) Mean movement speed (cm min-1 ± SD) for positive, negative and control trials of (A) *B. scalariforme*, (B) *C. granularis*, (C) *H. phrygiana*, and (D) *H. lisa* (note: vertical and horizontal axis scales are not equal across panels). Speed measurements were taken every 30 s and pooled into 5 min averages. Positive foods for *B. scalariforme* were (1) *G. verrucosa* and (2) detritus pellets. Positive foods for *C. granularis* were (1) *M. lingua* and (2) *G. verrucosa*. Positive foods for *H. phrygiana* were (1) *F. alabastrum* and (2) vegetal pellets. Positive foods for *H. lisa* were (1) *M. lingua*, (2) *Geodia* sp. and (3) *Iophon* sp. Stars indicate when contact was made with a positively scored food item. In panel D, multiple stars were used where replicates for the same food type had notably different initial contact times.

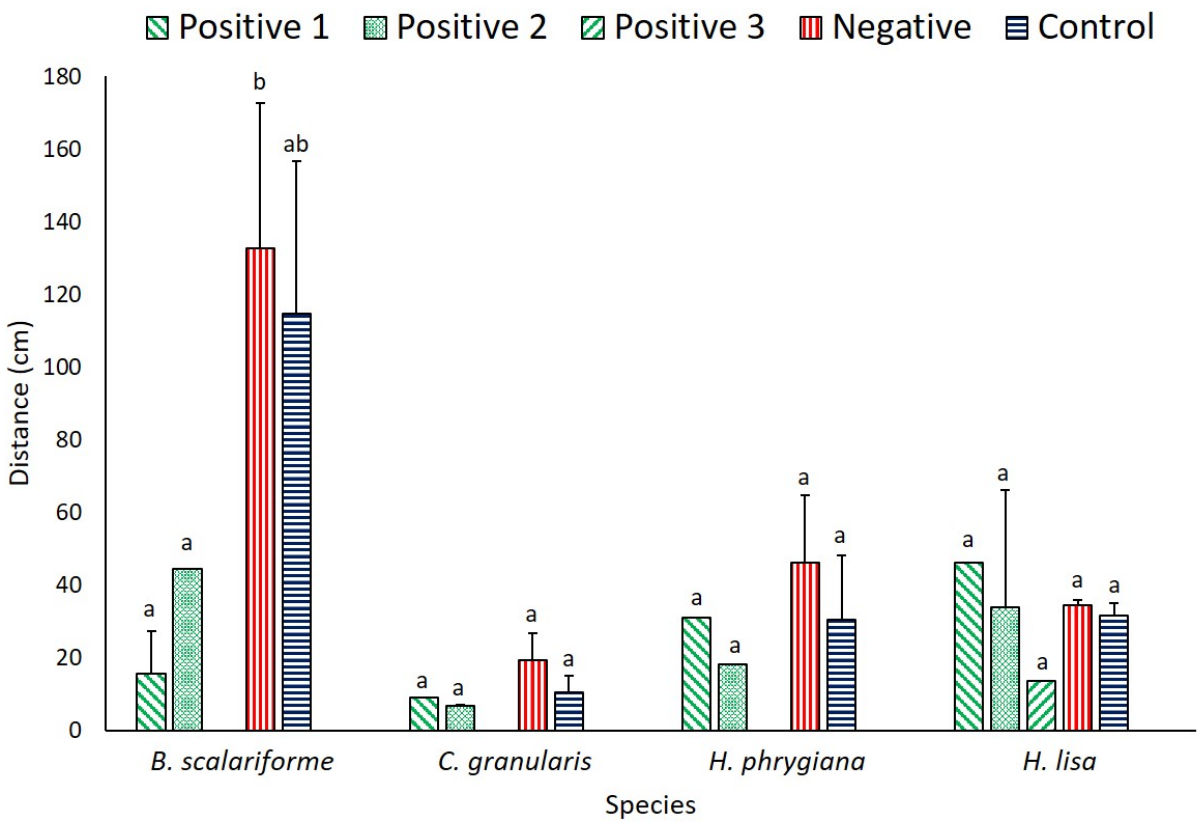

Figure 2.5 Mean distance traveled in cm (± SD) by individuals of *B. scalariforme, C. granularis, H. phrygiana*, and *H. lisa* during positive, negative, and control trials. Immobile trials (< 1 body length of movement) were excluded from this analysis. Positive foods for *B. scalariforme* were (1) *G. verrucosa* and (2) detritus pellets. Positive foods for *C. granularis* were (1) *M. lingua* and (2) *G. verrucosa*. Positive foods for *H. phrygiana* were (1) *F. alabastrum* and (2) vegetal pellets. Positive foods for *H. lisa* were (1) *M. lingua*, (2) *Geodia* sp. and (3) *Iophon* sp. Distances were compared within species for different response types; bars marked with different letters were determined to be statistically significant, $p < 0.05$ (see text for full results).

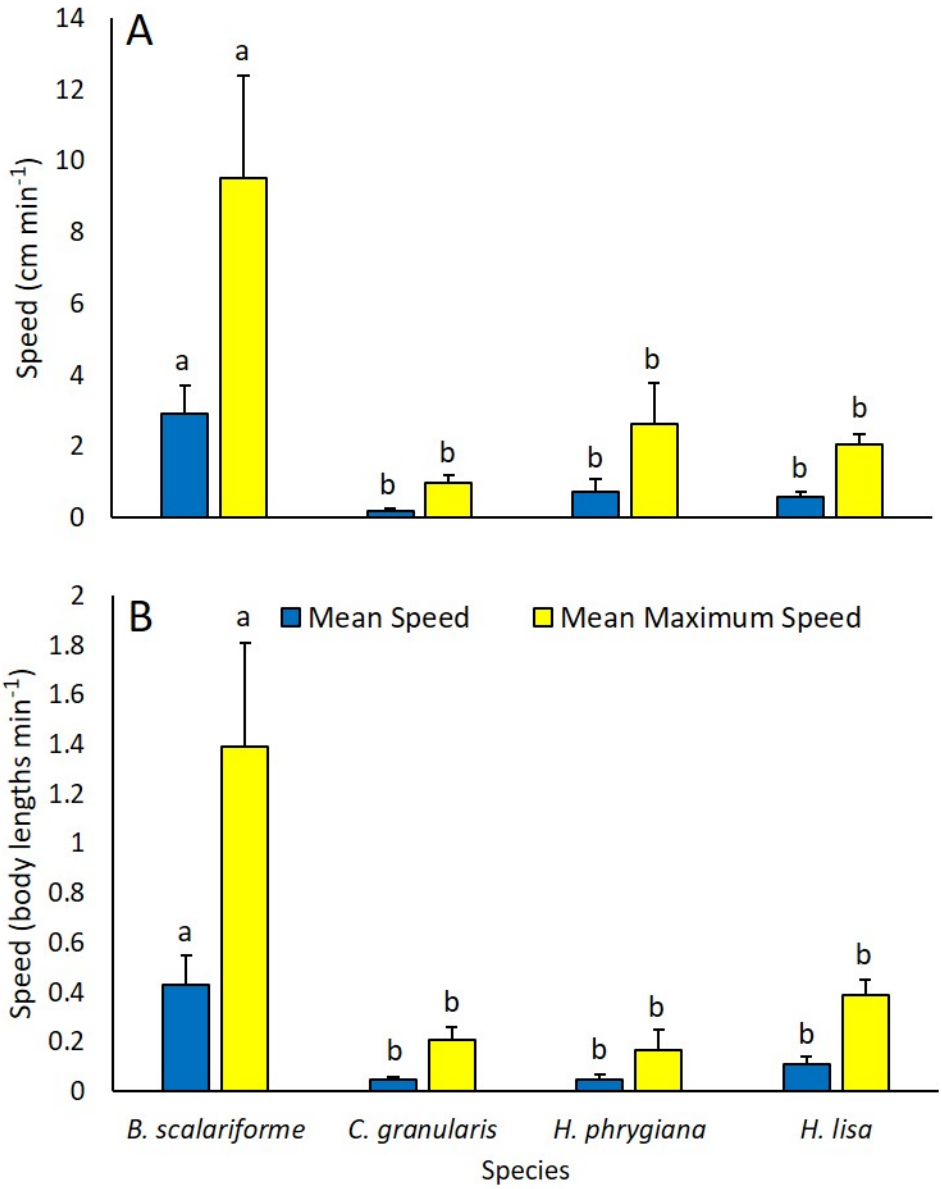

Figure 2.6 Mean and mean maximum speeds (± SD) exhibited by *B. scalariforme, C. granularis, H. phrygiana*, and *H. lisa* during foraging measured as either (A) absolute speed (cm min^{-1}) or (B) relative speed (body lengths min^{-1}). Individuals that remained immobile (< 1 body length of movement) were excluded from analysis. Speeds were compared between species for each speed type (mean or mean maximum). Different letters represent bars of the same type (mean or maximum speed) that were significantly different, $p < 0.05$ (see text for full results).

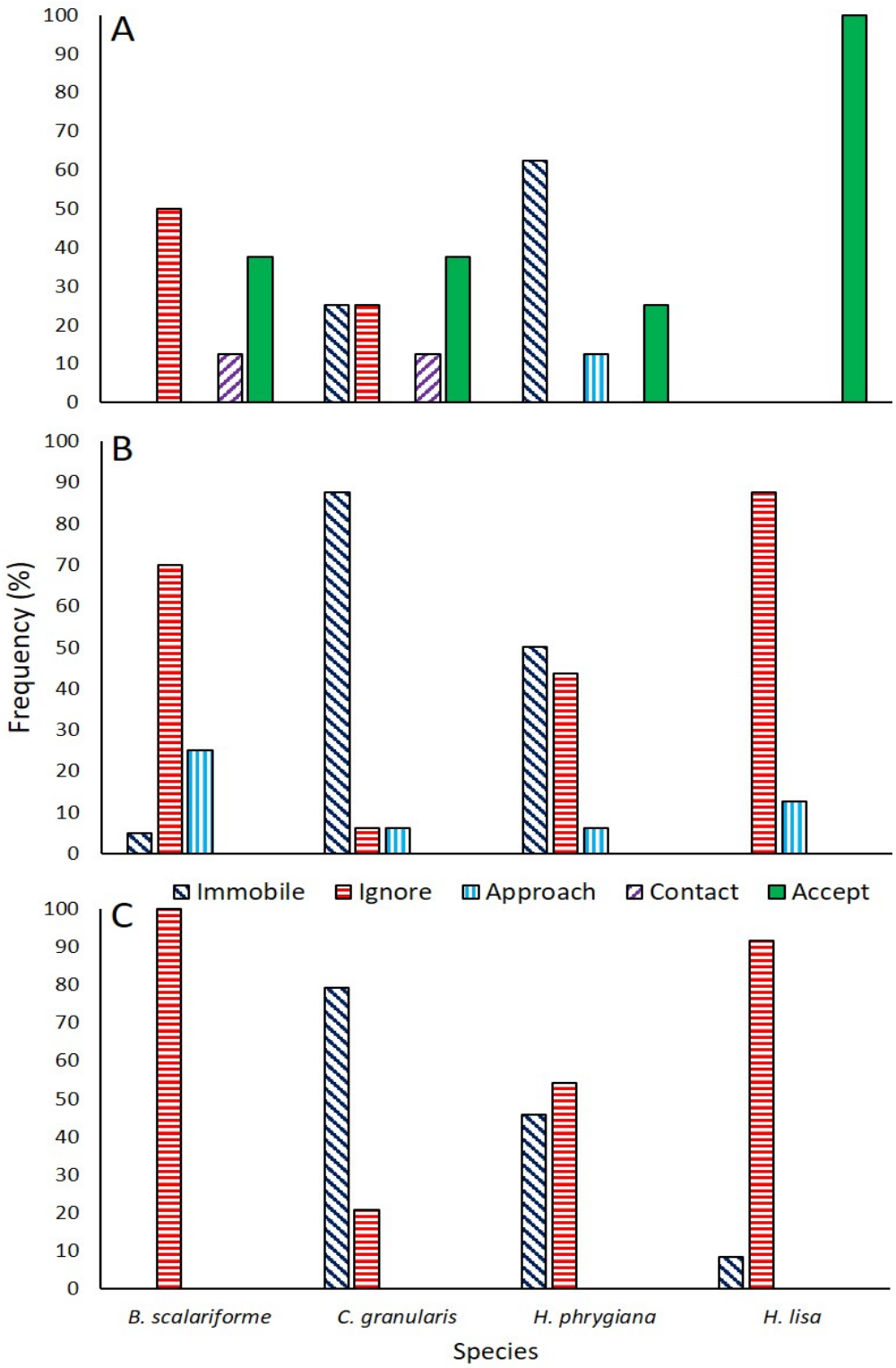

Figure 2.7 Percent frequency of behaviour scores for *B. scalariforme*, *C. granularis*, *H. phrygiana*, and *H. lisa* during (A) positive trial replicates, (B) negative trial replicates, and (C) control trial replicates.

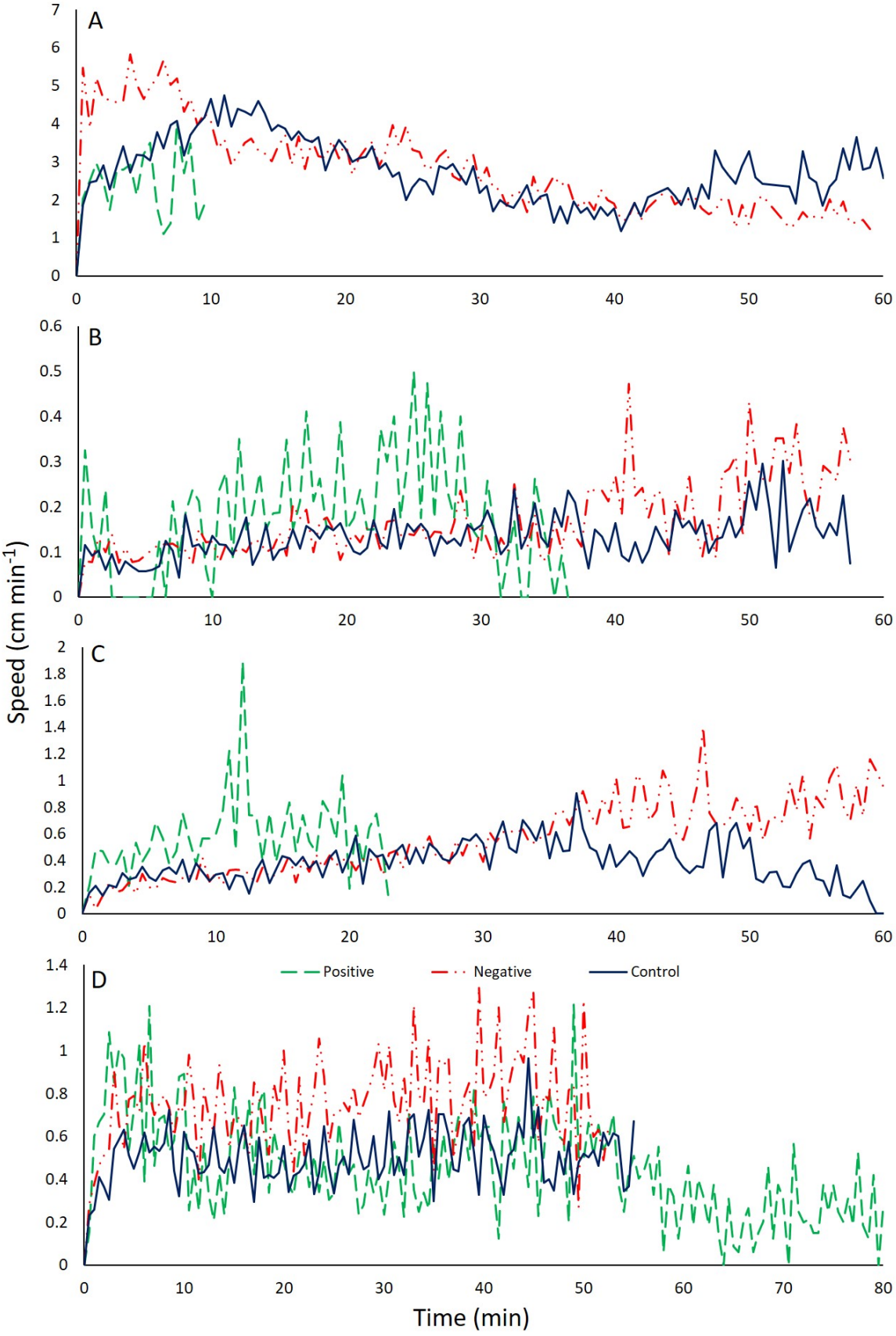
A
B
C
D
Positive
Negative
Control
Speed (cm min-1)
Time (min)

Figure 2.8 (previous page) Variability in movement speed for (A) *B. scalariforme*, (B) *C. granularis,* (C) *H. phrygiana*, and (D) *H. lisa* in positive, negative, and control trials (30 s intervals, all replicates of each response type compiled and mean speed for each data point provided). Note that vertical and horizontal axis scales are not all equal.

2.9 Supplementary Material

2.9.1 Supplementary Tables

Table S 2.1 Response metrics measured for each focal species in the positive, negative and control trials. Results expressed as mean ± S.D; r is provided for angular data representing how tightly values were clustered around the mean.

	B. scalariforme	***C. granularis***	***H. phrygiana***	***H. lisa***
Response Time (min)	8.9 ± 3.0	34.8 ± 0.5	21 (cup coral) 80 (vegetal pellets)	63.0 ± 24.78
Positive Travel Angle (°)	195.5 ± 13.5 r = 0.97	173.4 ± 11.9 r = 0.98	172.8 ± 9.0 r = 0.99	175.4 ± 27.8° r = 0.89
Negative Travel Angle (°)	91.5 ± 114.5 r = 0.14	21.4 ± 87.0 r = 0.32	7.4 ± 121.7 r = 0.11	43.6 ± 75.5 r = 0.42
Control Travel Angle (°)	131.5 ± 82.9 r = 0.35	336.4 ± 106.9 r = 0.18	353.0 ± 110.5 r = 0.16	345.0 ± 106.8 r = 0.18
Mean Speed (cm min^{-1})	2.9 ± 0.8	0.2 ± 0.1	0.7 ± 0.4	0.6 ± 0.1
Maximum Speed (cm min^{-1})	9.5 ± 2.7	1.0 ± 0.2	2.6 ± 1.2	2.0 ± 0.3
Positive Period (min)	1.75 ± 0.7	1.6 ± 0.7	1.6 ± 0.7	1.44 ± 0.42
Negative Period (min)	1.6 ± 0.7	1.5 ± 0.6	1.5 ± 0.6	1.52 ± 0.48
Control Period (min)	1.5 ± 0.5	1.6 ± 0.5	1.5 ± 0.5	1.57 ± 0.63
Maximum Amplitude (cm min^{-1})	2.7	0.33	1.4	1.02
Positive Amplitude (cm min^{-1})	1.88 ± 0.81	0.20 ± 0.07	0.47 ± 0.37	0.31 ± 0.17
Negative Amplitude (cm min^{-1})	0.67 ± 0.29	0.10 ± 0.12	0.18 ± 0.15	0.33 ± 0.21
Control Amplitude (cm min^{-1})	0.57 ± 0.30	0.07 ± 0.05	0.17 ± 0.12	0.20 ± 0.12

2.9.2 Supplementary Figures

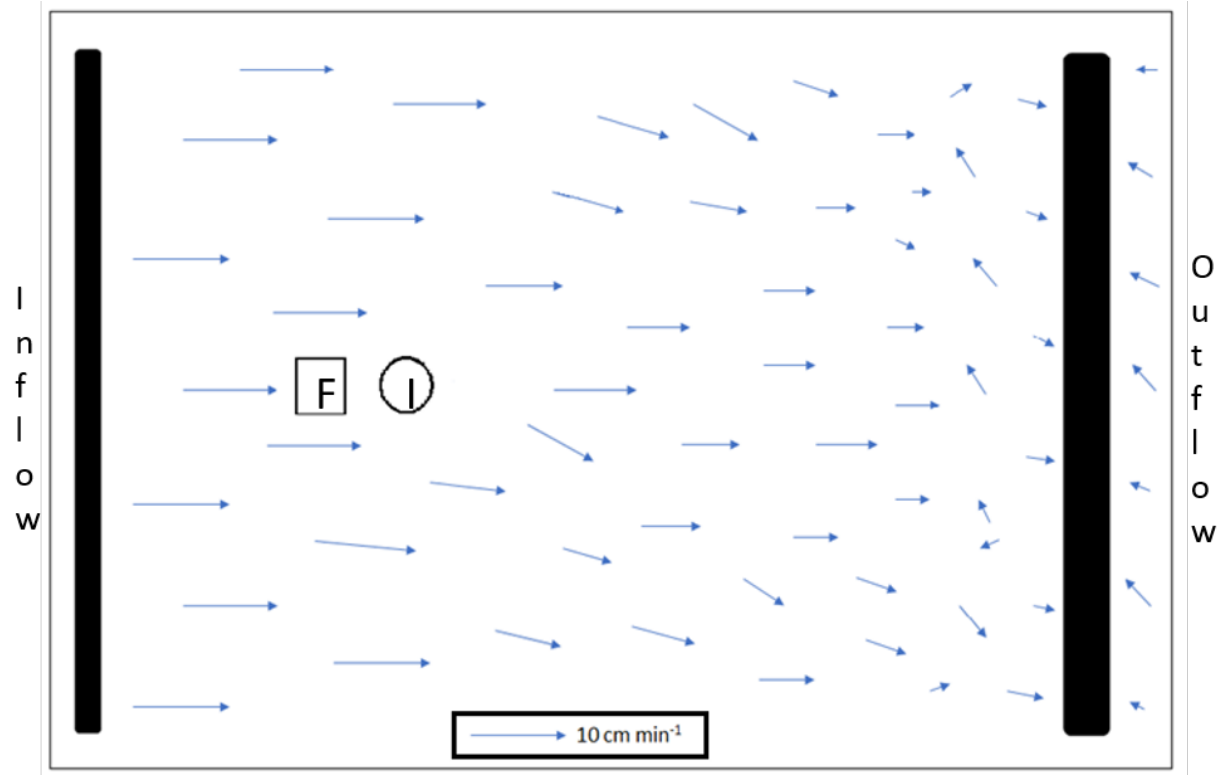

Figure S 2.1 Diagram of general flow patterns in the experimental arena. Vectors are scaled to reflect current velocity at a given point in the tank relative to the vector provided at the bottom. Inflow was continuous for the duration of the experimental trials. The square is the general area of food (F) placement during trials and the circle is where the experimental individual (I) was placed (~1 body length from food). Inflow and outflow pipes are as labeled and to scale.

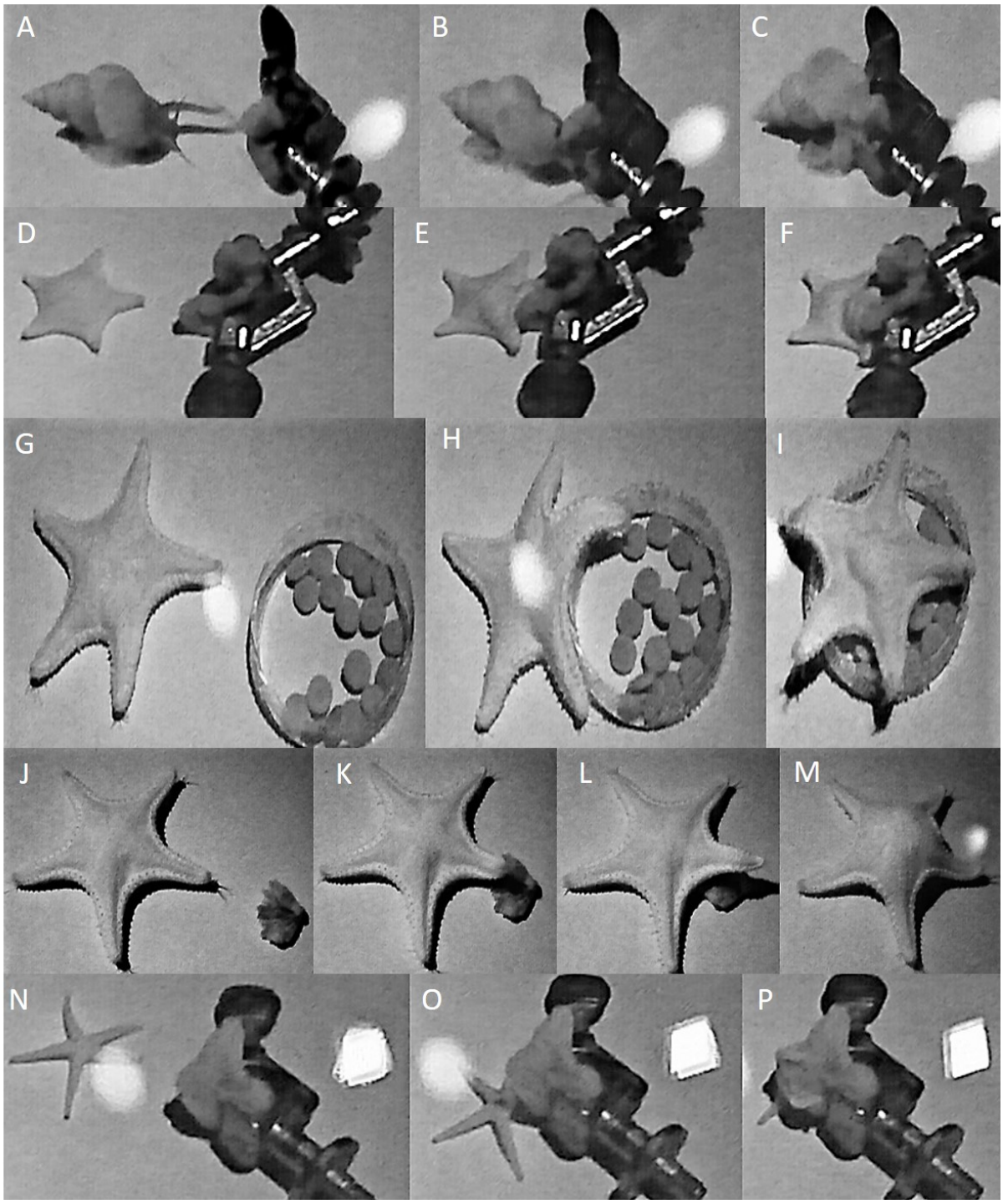

Figure S 2.2 Focal species approaching food items. *B. scalariforme* (A) approaching, (B) making initial contact with, and (C) feeding on a chunk of octopus. *C. granularis* (D) approaching, (E) making initial contact with, and (F) feeding upon a chunk of octopus, *H. phrygiana* (G) approaching, (H) making initial contact with, and (I) feeding on vegetal pellets, *H. phrygiana* (J) approaching, (K) making initial contact with, (L) making fuller contact with, and (M) feeding on a sample of *F. alabastrum*, *H. lisa* (N) approaching, (O) making initial contact with, and (P) feeding on a sample of sponge.

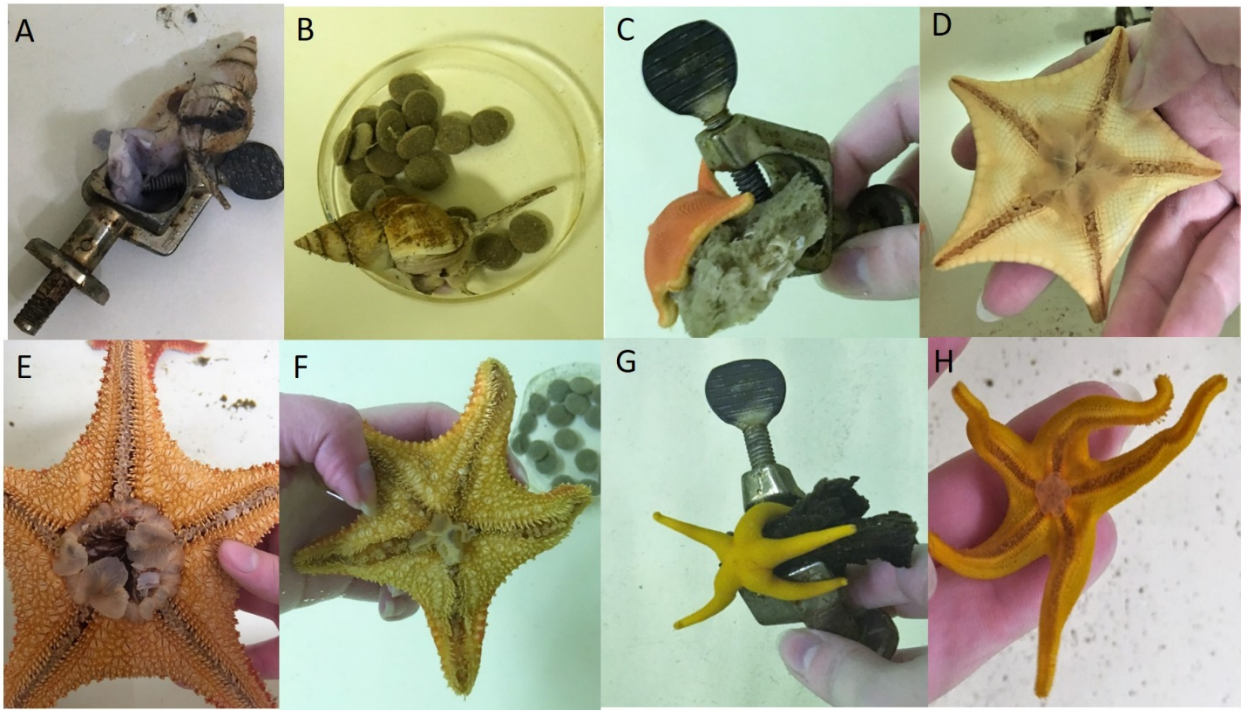

Figure S 2.3 Feeding postures and evidence of feeding from laboratory trials of focal species. (A) *B. scalariforme* feeding on a piece of octopus tentacle. (B) *B. scalariforme* feeding on mixed organic detritus pellets. (C) *C. granularis* adopting a feeding posture on a sample of *M. lingua*. (D) Oral surface of *C. granularis* revealing eversion of stomach after coming in contact with a piece of octopus tentacle. (E) Oral surface of *H. phrygiana* revealing eversion of stomach surrounding a sample of *F. alabastrum*. (F) Oral surface of *H. phrygiana* revealing eversion of stomach after coming in contact with vegetal pellets. (G) *H. lisa* adopting a feeding posture on a sample of *Iophon* sp. (H) Oral surface of *H. lisa* revealing eversion of stomach after coming in contact with a sponge.

2.9.3 Supplementary Videos

Videos are available through Memorial University's research repository

Video S2.1: *B. scalariforme* displaying siphon sweeping behaviour

Video S2.2: *H. phrygiana* approaching and feeding upon vegetal pellets

Video S2.3: *H. phrygiana* approaching and feeding upon coral

Video S2.4: *H. lisa* approaching and feeding upon sponge

Chapter 3 Intraspecific and interspecific interactions in deep-sea gastropods and sea stars in response to food

3.1 Abstract

Competitive interactions come in a variety of forms and may be modulated by the species involved, the size and number of individuals, and/or the resources available. While competition for limited food resources in the deep sea is expected to occur, most studies to date have focused on broad community responses to baits (pelagic taxa) and food falls (pelagic and benthic taxa), rather than on foraging patterns and species-specific attributes. Here, intra- and interspecific competitive behaviours for food were experimentally studied in four deep-sea benthic species from the western North Atlantic in multi-animal competitive trials (2, 3, or 5 individuals) and two simulated food fall experiments involving the four species simultaneously. The sea star *Ceramaster granularis* displayed a range of competitive and cooperative behaviours depending on competitor identity (conspecific or heterospecific), size (similar size or differing sizes), and number of individuals present. The sea star *Hippasteria phrygiana* displayed competitive behaviours towards conspecifics where larger individuals outperformed smaller ones, and either competitive or predatory behaviours towards the gastropod *Buccinum scalariforme*. The sea star *Henricia lisa* displayed little to no interaction with conspecifics and was frequently outcompeted at food sites by *C. granularis*. The gastropod *B. scalariforme* showed competitive behaviour towards conspecifics and potentially kleptoparasitic behaviours towards *H. phrygiana*. Comparing the present results to those obtained in previous singleton studies suggests that *C. granularis* responds to food cues fairly consistently (in terms of delay and speed) regardless of presence or absence of competition, *H. phrygiana* responds more slowly in the presence of competition, *H. lisa* responds to food cues more quickly when potential competitors are present,

and *B. scalariforme* responds to food cues more slowly on average in the presence of competition (showing two distinct styles of approaching food items). Large individuals did not always outcompete smaller individuals, and faster species did not always outcompete slower species, highlighting the complexity of interactions in deep-sea benthic environments.

3.2 Introduction

Competitive interactions between individuals (both conspecifics and heterospecifics) can have a profound impact on feeding rates and behaviours (Gaymer et al., 2002; St-Pierre et al., 2018). Such interactions may be direct, such as fighting or kleptoparasitism (food stealing; Rochette et al., 2001) or indirect (e.g. exploitative, one individual using a shared resource before the other can; Menge & Menge, 1974; Schmitt, 1987). When considering the effects of competition on the ability of marine predators to hunt and feed, morphological (e.g. size) and physiological (e.g. hunger state) traits may give certain individuals competitive advantages over others when resources are limited, as seen in previous studies involving crustaceans, bivalves, gastropods, and echinoderms (e.g. Menge, 1972; Schmitt, 1987; Sbragaglia et al., 2017; Rogers et al., 2018; St-Pierre et al., 2018; Liu et al., 2019).

Studies of competitive relationships among most marine taxa, including asteroid echinoderms (sea stars), have so far been centered on shallow-water benthic ecosystems. Menge and Menge (1974) determined that *Pisaster ochraceus* was aggressive towards *Leptasterias hexactis*, thereby reducing the time it spent foraging. Rogers et al. (2018) likewise found evidence of *P. ochraceus* being aggressive and dominant over another sea star, *Evasterias troschelii*, inducing avoidance behaviours. Two competing sea stars of the genus *Astropecten*, *A. aranciacus* were found to frequently prey upon *A. bispinosus* in addition to competing for shared food resources, and it was determined that *A. aranciacus* was most effective when preying upon

buried rather than mobile individuals of *A. bispinosus* (Schmid & Schaerer, 1981). Other studies have suggested that predators across taxa may compete for shared prey resources. For example, Morissette and Himmelman (2000) observed that when the sea star *Leptasterias polaris* fed upon the clam *Spisula polynyma* it frequently suffered from kleptoparasitism from the sea star *Asterias rubens* (as *A. vulgaris*), the whelk *Buccinum undatum*, and the crabs *Hyas araneus* and *Cancer irroratus*. Females of the whelk *B. undatum* were determined to be more likely than males to kleptoparasitize the prey of *L. polaris* prior to egg laying, potentially due to the reproductive benefits of securing extra food despite the predation risk the sea star posed (Rochette et al., 2001). St-Pierre et al. (2018) found that the identity of a competitor could modulate the foraging behaviour of *Asterias rubens*. The latter prioritized consumption of prey over responding to contact initiated by crabs, i.e. altering consumption and feeding behaviour in the presence of *C. irroratus* and increasing movement speeds in the presence of *C. maenas*. While such examples abound for shallow-water taxa, the potential influence of competition between megafaunal predators (both intraspecifically and interspecifically) has not been extensively studied in deep-sea species.

Whelks of the genus *Buccinum* are typically known to be either active predators or scavengers, preying upon polychaetes, bivalves, sea urchins, and scavenging upon various species of fishes (such as those killed by beam trawling), and opportunistic kleptoparasites (Himmelman & Hamel, 1993; Evans et al., 1996; Morissette & Himmelman, 2000; Ilano et al., 2005). Work involving deep-sea members of the genus is limited to *B. yoroianum* and *B. scalariforme*, which show prominent scavenging tendencies upon a variety of prey types (fish, cephalopod, and detritus; Aguzzi et al., 2012; Stuckless et al., in submission; see Chapter 2). Similarly, information regarding the diets and behaviour of deep-sea sea stars is limited when

compared to their shallow-water counterparts. In nearshore environments, sea stars are frequently described as keystone predators, especially in rocky subtidal ecosystems, feeding upon various molluscs, bivalves, and occasionally other echinoderms (e.g. Schmid & Schaerer, 1981; Gaymer et al., 2002; Wong & Barbeau, 2003; Hummel et al., 2011; Gooding & Harley, 2015). Gale et al. (2013) and Stuckless et al. (in submission) studied the diet of several deep-sea sea stars such as *Ceramaster granularis*, which is a sponge eater and scavenger of various types of carrion, *Hippasteria phrygiana,* which is a prominent predator of cnidarians with potential for detritivory, and *Henricia lisa,* which is a spongivore and also appears to display opportunistic scavenging. However, so far nothing appears to have been done regarding potential competition within or between any of these co-occurring species.

Whether or not deep-sea species are subject to various forms of competition from conspecifics and co-occurring species and whether any hierarchies exist within these interactions has not been well studied. In addition, possible gregarious dynamics among conspecific individuals such as group foraging, or size asymmetric competition are also understudied. The present study pursued the main objective of exploring species interactions of deep-sea species in response to food under competitive settings. Diets and foraging strategies previously determined under non-competitive settings (Stuckless et al., in submission) were tested in the presence of conspecifics (with varying numbers of individuals and differences in their body sizes) and among individuals belonging to different species. The main hypotheses tested were that: (1) larger individuals would outcompete smaller individuals of the same species for access to a limited food source due to increased strength and/or movement speed (Montgomery & Palmer, 2012; Hemmert & Baltzley, 2016), and (2) faster species would outcompete slower species.

3.3 Materials and Methods

3.3.1 Collection and Holding Conditions

The four focal species are common in the deep sea of the Northwest Atlantic and are the same as seen in Chapter 2. The gastropod *B. scalariforme* is found between subtidal and bathyal depths (>1100 m) off Greenland and Iceland, the Arctic Ocean, Alaska (USA), along both coasts of Canada, and Maine (USA) (Montgomery et al., 2017). The sea star *C. granularis* colonizes depths ranging from ~50 to >1400 m in the Arctic Ocean and on both sides of the North Atlantic Ocean, to as far south as the Northeast coast of South America (Gale et al., 2015; Mah, 2019a). The sea star *H. phrygiana* is a found throughout the Northern and Southern Atlantic and Pacific oceans ranging between 10 and 1400 m depth (Mah et al., 2014). Meanwhile, the sea star *H. lisa* is reported in deep waters of the North Atlantic basin down to ~1400 m (Mah, 2019b).

Individuals of each species were collected as opportunistic trawl by-catch between 2013 and 2017, during routine surveys conducted by Fisheries and Oceans Canada (DFO) off the eastern coast of Canada between 800-1500 m depths. Collections took place in late autumn and early winter to ensure that surface temperatures were within tolerable ranges for deep-sea species (typically between 1-6 °C) to minimize thermal shock during surfacing. Individuals were kept alive in onboard tanks and then relocated to the Ocean Sciences Centre where they were housed at atmospheric pressure in dark flow-through tanks supplied with ambient seawater (fluctuating between 0-8 °C over the course of the year). All focal species appeared to tolerate atmospheric pressure well, with records of feeding, growth, and reproduction in mesocosms (Mercier & Hamel, 2008; Gale et al., 2013; Montgomery et al., 2017). Holding mesocosms had ~15-20 cm of muddy substrate available along with some rocks and deep-sea corals and focal species were housed communally except for most of the individuals of *H. phrygiana*, which were kept

together in a separate tank to prevent unplanned predation on cnidarians as per Gale et al. (2013). All individuals were acclimated to the laboratory mesocosms (minimum of several months) before using them for experiments and only individuals determined to be responsive, active, and in healthy condition, without any visible lesions or injuries were chosen for the experiments. Outside of the experimental phase, individuals were fed weekly with chunked mussels (*Mytilus edulis*), sea urchins (*Strongylocentrotus droebachiensis*), and scallops (*Placopecten magellanicus*), as well as with fresh or thawed sponges, shrimps and other preys collected from the deep sea on an opportunistic basis.

3.3.2 Experimental Conditions

Experiments were conducted in two 320-L tanks (80 cm wide x 126 cm long x 29 cm deep). A LED infrared light (DC 12V) was mounted above each tank along with infrared sensing cameras (Brinno TLC 200 Pro and MAC 200 DN) so that the field of view encompassed the entire tank. Cameras were set to take one picture every 30 s; photos were automatically stitched together into a video clip. An additional camera (Brinno TLC 200 Pro) was placed at the edge of the experimental tank with a field of view focused on the food item to record finer-scale interactions or precise behaviours. This camera took one picture every 10 s to generate a video clip (as above). This set up is the same as used in Stuckless et al. (in submission; see Chatper 2).

Running ambient seawater (31.5 L min^{-1}) was provided through a T-shaped pipe placed 5 cm above the tank bottom with holes drilled along one side every ~2 cm to create a unidirectional inflow; a similarly-shaped drain with holes drilled ~2 cm apart along its surface on all sides was placed at the other end, 25 cm from the tank bottom, to facilitate uniform and laminar flow/outflow. Flow strengths across the experimental arena (≤10 cm sec^{-1}) were measured using a handheld flow probe (Hoskin Scientific Flow Meter FP211) and flow

directions were measured by injecting ~0.3 mL of food dye at various points near the bottom of the tank. Dominant currents in the experimental tanks are described in Supplementary Figure S2.1. Experimental tanks had no substrate as all focal species had been observed willingly occupying hard substrate surfaces in the holding mesocosms and in prior studies (preliminary observations and Stuckless et al., in submission).

Four replicates (except where otherwise noted for long duration trials) of each experimental and control treatment were run. In every set of four replicates, each of the two tanks were used twice for treatments and twice for controls in an attempt to minimize tank effects. If only two replicates were performed (as is the case for some long duration trials, described below) then each tank was used once for each treatment type. In addition, the direction of water flow was opposite in the two tanks to help control for any environmental effects. Between each trial, tanks were emptied of water, scrubbed, and refilled between trials to prevent any buildup of cues from stimuli or other animals. The tanks were filled with ambient, unfiltered seawater and allowed to flow for 10 min once they were refilled after a cleanup before a stimulus was placed in the tank. Individuals of the focal species were introduced to the tank 5 min later; this allowed time for any scent plumes to form where applicable as per Stuckless et al. (in submission). A variety of deep-sea preys previously determined to be palatable to the focal species based on prior work (Stuckless et al., in submission) were used as food stimuli: chunks of tentacle from the deep-sea octopus *Graneledone verrucosa*, the cup coral *Flabellum alabastrum*, and several species of deep-sea sponges (*Mycale lingua*, *Iophon* sp., and *Asconema* sp.). All food items used weighed between 8-12 g and were held in place by a small stainless-steel clamp where required to prevent movement of food in the tank current as seen in Stuckless et al. (in

submission). In the case of control trials, a small grey polyresin aquarium decoration of similar size to the food items was placed in the control tank.

Short duration experimental trials (6-78 min) were run to assess competition between individuals during brief/acute responses to food stimuli. Trials ended when one of the predetermined end conditions were met: (1) no movement from any individual for 30 min after onset of a trial (this delay was determined to predict long-term immobility in preliminary trials), (2) no individual began to approach the stimulus within 60 min of trial onset, (3) an individual approached food (< 0.5 body lengths away) and then moved away with no second approach within 10 min and no other individuals approaching, and (4) an individual attempted to consume the food. End conditions were adapted from Gale et al. (2013) and Stuckless et al. (in submission). All individuals were fasted for a minimum of two weeks prior to experimental trials as per Gale et al. (2013) and Stuckless et al. (in submission). Individuals were observed in real time as well as through time-lapse videography until contact was made with the food item and a feeding posture was adopted (with stomach eversion in some cases). The trial was interrupted before feeding took place to preserve food items (especially rare deep-sea prey used in other laboratory studies) and the hunger state of the individuals used. The time taken for individuals to reach a food item and assume feeding behaviours/postures (if this happened), as well as the path the individuals took over the course of the trial, were recorded along with other possible interactions and any behaviour of note.

Prolonged trials were run to examine effects of competition between individuals beyond the initial detection of food and the time taken to reach food and adopt feeding postures. Prolonged trials were allowed to run freely for 18-23 h (depending on the trial) and any feeding that took place was only interrupted by the investigator at the end of the trial duration. Any

individuals that fed during the trial duration were not used in another trial for two weeks in order to ensure that individuals were hungry again before the next trial. This period of time is unlikely to cause the individuals any harm, as determined by studies on other species of sea stars and gastropods (Rochette et al., 1994; Drolet & Himmelman, 2004; Lau & Leung, 2004; Gale et al., 2013; Tamburi & Martin, 2016).

Experimental individuals for both short and prolonged duration trials were measured while submerged after the completion of each trial, in an attempt to minimize any behavioural artefacts from pre-trial handling on experimental results. Sea star radii were measured using a piece of string and a ruler. Three arms were chosen haphazardly for each individual to be measured from the center of the disk to the tip of the arm along the dorsal surface and the average was calculated. For gastropods, the length of the shell was measured from the apex to the bottom edge of the aperture, using string and a ruler. Once all the experiments were completed, a subset of the individuals used in the experiments were haphazardly chosen from the holding mesocosms and measured for diameter/shell length and weighed (wet weight) using a scale (Ohaus Scout Pro 2000) after being gently blotted dry with paper towels (data on diameter/shell length to weight are available in Supplementary Figure S3.1). After weighing, individuals were returned to the holding mesocosms. During weighing, photos were taken of the oral side of sea stars for further measurements to be taken using ImageJ. The area (cm^2) of the oral opening was measured, along with the area (cm^2) of the oral surface covered by the ambulacral groove, which was used as a proxy for the area of oral surface covered by podia, as podia were generally withdrawn into the ambulacral groove (and sometimes covered by spines) when taken out of the water, and thus, podia could not be clearly measured. The area (cm^2) of oral surface not composed of the ambulacral groove/podia or oral opening (termed ‘webbing

area') was also measured using the circle and polygon tools, as appropriate. From these measurements, a percent area covered by ambulacral groove (i.e. podia) was calculated for each individual and then averaged for each species of sea star (mean ± SD, Supplementary Table S3.1).

Individuals were kept constantly submerged and in the dark as much as possible while being transferred between holding tanks and experimental setups. No animal was used twice in the span of 48 h in an attempt to lower handling stress, and replicates were interspersed among focal species to minimize the bias of temporal variations on interspecific comparisons; all replicates of a given treatment were run within four weeks of each other. Conspecific and interspecific interaction experiments ran from March to July 2018 while food fall experiments in the mesocosm were conducted from December 2018 to January 2019.

3.3.3 Treatments

3.3.3.1 Presence of Conspecifics

The food stimulus used in trials involving similarly sized and differently sized individuals of *C. granularis* was a chunk of tentacle from the deep-sea octopus *Graneledone verrucosa*. The cup coral *Flabellum alabastrum* was the food stimulus in trials with *H. phrygiana,* whereas in trials with *H. lisa* various species of deep-sea sponges were used (*Mycale lingua*, *Iophon* sp., or *Asconema* sp.). A chunk of tentacle from the deep-sea octopus *G. verrucosa* was used as food stimulus in trials involving *B. scalariforme*. Palatable food types were determined for each focal species during another study (Stuckless et al., in submission).

Trials were run for all four focal species to assess interactions between conspecifics (in various combinations of numbers and body sizes) during exposure to a limited food source. Two individuals of the same species of similar size (≤ 25% difference in size, Table 3.1) were placed

~5 cm from each other and ~1 body length down current from a food item (described above). Another experiment tested two conspecifics of different sizes (> 30% difference, Table 3.1) with each of *C. granularis* and *H. phrygiana* (as the number of individuals available for these species provided individuals of a greater variety of sizes). In addition, experiments with five conspecifics of varying sizes were run using the same two species (Table 3.1), with a prolonged duration (18-23 h) to examine the potential effects of exposure to competitive situations beyond initial exposure to/detection of food items. Using the same experimental setup, the five individuals for this trial were placed more closely together (~1-3 cm apart) and in a semi-circular formation approximately one body length down current from the stimulus. The ratio of animal wet weight to food wet weight for each type of trial is available in Table 3.2.

3.3.3.2 Presence of Multiple Species

As the focal species in these experiments have overlapping geographical and depth ranges of occurrence (Gale et al., 2015; Murillo et al., 2016) they may be found in the same precise location and trials were run to determine interspecific interactions (competition) in response to the presence of a limited food source using the same set up as described previously.

Palatable food types were determined for each focal species during another study (Stuckless et al., in submission). The food stimulus used in short duration trials of *C. granularis* and *H. lisa* together were samples of deep-sea sponges (*Mycale lingua*, *Iophon* sp., or *Asconema* sp.). The food stimulus used in short duration trials of *C. granularis* and *B. scalariforme* together consisted of chunks of tentacle from the deep-sea octopus *G. verrucosa*. Samples of deep-sea sponges (*M. lingua* or *Iophon* sp.) were used as the food stimuli for prolonged duration trials testing individuals of *C. granularis* and *H. lisa* simultaneously. Chunks of tentacle from the deep-sea octopus *G. verrucosa* were used as the food for prolonged duration trials testing

individuals of *C. granularis* and *B. scalariforme* as well as for prolonged trials testing individuals of *C. granularis*, *H. lisa*, and *B. scalariforme* simultaneously (since additional information available by this time suggested that *G. verrucosa* was palatable carrion to *H. lisa* as well).

Two individuals, i.e. one individual of two focal species in combination (either *C. granularis* and *H. lisa,* or *C. granularis* and *B. scalariforme*), were placed in the experimental tank ~5 cm from each other and ~1 body length down current from a food item that had been determined to be of interest to both species, as detailed above. An additional two replicates of each type of interspecific experiment were run with a prolonged duration (~18-23 h) to assess additional interactions or behaviours that might occur beyond the initial food detection and acquisition (e.g. displacing of competitors on a food item) with one control and one experimental treatment taking place in each tank. Additional experiments were also run using three individuals, one each of a differing species (*C. granularis, H. lisa,* and *B. scalariforme*), placed side-by-side in the experimental tank ~1 body length down current from a shared food item. Experimental set up was as above, there were four replicates and trials ran with a prolonged duration (~18-23 h). The ratio of animal wet weight to food wet weight for each type of trial is available in Table 3.2.

3.3.4 Simulated Food Falls

This study was conducted in a dark, cylindrical mesocosm (800 L capacity with a flow of 0.95 L min^{-1}, and a 12-15 cm layer of soft sediment) to simulate complex interactions during a pulse of food availability. Two food falls were simulated, one involving an Atlantic salmon (*Salmo salar*) sliced open along the ventral side, and another involving the head of a deep-sea octopus (*G. verrucosa*) with the tentacles removed that Stuckless et al. (in submission)

determined to be palatable. The mesocosm community consisted of 15 *C. granularis*, 9 *H. phrygiana*, 8 *H. lisa*, 6 *B. scalariforme*, and several other species including: 8 *Stephanaster albula*, 1 *Crossaster papposus*, four unidentified gastropods, and an indeterminate number of brittle stars (*Ophiopholis aculeata* and *Ophiura* sp.) and unidentified infaunal polychaetes. The tank was not fed (except for any particulate matter coming in with the unfiltered seawater) for five weeks prior to the addition of the first food fall (salmon) and then fasted for one week (due to time constraints) before the beginning of the octopus food fall. Given that shallow-water sea stars and gastropods are not negatively affected by weeks/months of fasting (Rochette et al., 1994; Drolet & Himmelman, 2004; Lau & Leung, 2004; Gale et al., 2013; Tamburi & Martin, 2016) food deprivation over this time period was unlikely to be harmful to deep-sea counterparts, which presumably feed sporadically *in situ*. The salmon food fall (2820 g) was recorded for 12 consecutive days in December 2018, and the remainder of the salmon (final weight 2792 g) was then removed from the mesocosm for inspection. The octopus food fall (initial weight 230 g) was recorded for 29 consecutive days between December 2018 and January 2019 until it was completely consumed/degraded. A LED infrared light (DC 12V) was mounted above the water in the holding mesocosm along with an infrared sensing camera (Brinno MAC 200 DN) so that the field of view encompassed the entirety of the simulated food fall. The camera was set to take one picture every 30 s; photos were automatically stitched together into a video clip by the camera software.

3.3.5 Response Variables and Data Processing

Short-term experimental videos were analyzed frame by frame using the ImageJ plug-in MtrackJ (Meigering et al., 2012) to determine the mean and maximum speed and the total distance traveled during each trial run for every individual. A second analysis was done on every

10 frames (5 min) to determine the average change in path angle for animals that approached and fed upon the food in short duration videos. Paths with an average angle change of ≤25° were considered straight while paths with an average angle change of >25° were considered curved. For prolonged duration trials where no frame-by-frame analysis was performed, the path of an individual that fed was observed and then determined to be straight or curved by the investigator. The reference point between frames to measure movement was the oral area in all species, i.e. the center of the disk in sea stars, and the head in gastropods. Experimental trials were scored as either negative or positive for an individual, based on whether it attempted to feed (positive) or not (negative), while all control trials were pooled together. For short duration trials, the first individual to reach the food was noted before the trial was ended. For prolonged duration trials, videos were watched, and the dominant behaviour of each individual was recorded for each hour of trial time, and the proportion of time each individual spent engaging in each category of behaviour was then determined. There were 6 categories of behaviour: immobile (less than ~1 body length of movement), mobile (> 1 body length of movement), contact animal (making physical contact with another animal), contact stimulus (making physical contact with the stimulus), feeding (adopting feeding postures/behaviours), and unknown (when the animal was not visible, such as when a drain or shadow obscured the view, results available in Supplementary Table S3.2). For food fall experiments, the number of individuals of the four focal species approaching and feeding upon each food type was recorded for each date by reviewing the footage. If an animal approached and adopted feeding postures/behaviours at the food fall, it was counted as a 'visit'. Any individual that was already feeding on the food fall when the date rolled over was not counted again, thus only 'new' individuals approaching the food fall were recorded for each date. As the entire tank was not in view of the camera, any

individual that approached the food fall from out of the field of view was counted as a 'new' individual, while any individual that disengaged from the food fall and remained on-screen before making contact again was not recounted.

3.3.6 Data Analysis

Values provided in-text are supplied as mean ± SD where appropriate except for response times, which are provided as the median ± SD (a more robust value against extreme outliers). Data were analyzed in MaxStat software (V 3.6). One-way analysis of variance (ANOVA) with post-hoc Tukey tests were run for trials involving two individuals of the same species (but only individuals of similar size in *C. granularis* and *H. phrygiana*), to compare responses (positive, negative, and control) for distance traveled, mean speed, and maximum speed; if data were non-normal or had unequal variance, a Kruskal-Wallis test with post-hoc Dunn's test was used instead. Two-way ANOVAs with post-hoc Tukey tests were run for trials involving two individuals of differing sizes for *C. granularis* and *H. phrygiana* to determine if size class and response had any affect on distance traveled, mean speed, or maximum speed. Two-way ANOVAs with post-hoc Tukey tests were run for short duration trials involving two different species to determine if response and/or species effected distance traveled, mean speed, or maximum speed. Where a significant interaction between factors occurred, one-way ANOVAs with post-hoc Tukey tests or unpaired t-tests were used as appropriate within factors. Kruskal-Wallis tests with post-hoc Dunn's tests were run for the simulated food falls to compare the average number of new visits from each species approaching and feeding on the food fall each day for each type of food fall (salmon or octopus) to determine which species (if any) were visiting the food fall most frequently. In addition, unpaired two-tailed t-tests or Mann-Whitney U tests (depending on normality and homoscedasticity of data) were run on the number of new

individuals approaching each type of food fall within species to determine if there was a significant difference in the number of individuals of a given species that interacted with the different food falls. All tests used a significance value of $p < 0.05$, although data analysis followed the principles of statistical clarity advocated by Dushoff et al. (2019).

3.4 Results

3.4.1 Ceramaster granularis

When two or more individuals were introduced together, most of the contacts between individuals across all three conspecific treatments (two same sized individuals, two differently sized individuals, and five individuals of varying sizes) involved only the tips of the arms or edges of the oral disk. As the number of conspecifics increased (from 2 to 5), so did the number of contacts when approaching food or feeding (0.5 ± 0.5 to 2.8 ± 1.3 contacts per trial). No monopolizing of the food by one individual was ever noted (including when large individuals were present). When two individuals of similar sizes were released together, they typically maintained their distance with each other (> 1 cm). Even when two individuals were feeding on the food item at the same time (one instance) contact was only with the tips of arms and brief (~5 min). When two individuals of differing sizes were tested together, interactions were similar to when two similar sized conspecifics were together, except for one instance where the large individual reached the food first the smaller individual (arriving second) attempted to push itself under the body of the large individual (Supplementary Video S3.1) gaining ~1 cm in 12 min to successfully access the food and enabling both individuals to feed. Such attempts to push or get under a conspecific (or otherwise) for access to food was dubbed ‘wedging’ for the purpose of this study. When five individuals of varying sizes were released together, an interception behaviour took place in half of the trials, wherein smaller individuals (i.e. small or medium size

class) moved into the path of a large individual attempting to approach a food item early in a trial (11-20 min from the start). While this smaller individual pushed against and blocked the path of the larger individual (3-16 min of contact) the other small or medium sea stars present approached the food without contact. The larger individual eventually abandoned its trajectory toward the food and moved away. The intercepting individual then joined the others at the food (Supplementary Video S3.2). When individuals approached food already occupied by conspecifics, behavioural interactions immediately on the food varied depending on the size of the feeding individual(s); wedging to dislodge a larger individual, or a more cooperative behaviour for small or medium feeders. During the latter, individuals initially touched arm tips and after 13-16 min the individual already on the food changed position, allowing the new individual access. Up to 4 individuals at a time coordinated position (Supplementary Video S3.2). In contrast, large individuals arriving after smaller individuals pushed small individuals off the food completely rather than rearranging positions (one instance, Supplementary Video S3.3).

In all three treatments involving different sizes and densities of sea stars, individuals typically approached food in straight paths with the arm closest to the food leading. In trials where paths were more complex (i.e. trials with 5 individuals) the arm pointing towards the food was not always the initial leading arm (i.e. when an individual engaged in the interception behaviour before approaching food). During movement, the leading arm changed to the arm currently closest to the food before approaching the food itself. When individuals responded positively to the food source, the response time was 21.0 ± 10.0 min for similar sized individuals, 40.0 ± 8.3 min for two individuals of differing sizes, and 45.0 ± 150.8 min for five individuals of varying sizes (Table 3.3). Individuals that did not approach the food in experimental trials, like

individuals in the control treatments, were largely stationary and when they did move, they showed no clear leading arm preferences (Table 3.4; Figure 3.1).

No statistically clear differences were detected in trials involving similarly sized sea stars for distance traveled ($F_{2,11} = 0.514$, $p = 0.612$), mean speed ($F_{2,11} = 0.928$, $p = 0.424$), or maximum speed ($F_{2,11} = 1.065$, $p = 0.378$; Figure 3.1 A, B). Likewise, in trials involving two differently sized sea stars, size and response type did not clearly influence any of the metrics (Figure 3.1 C, D): i.e. distance travel traveled ($F_{1,19 \text{ and } 2,18} = 0.94$ and 2.46, $p = 0.121$ and 0.349), mean speed ($F_{1,19 \text{ and } 2,18} = 0.50$ and 1.93, $p = 0.491$ and 0.18) and maximum speed ($F_{1,19 \text{ and } 2,18} = 2.985$ and 1.001, $p = 0.106$ and 0.392).

3.4.2 Hippasteria phrygiana

As conspecific density increased (from 2 to 5 individuals) the number of interactions increased from 0.3 ± 0.5 to 3.0 ± 1.6 contacts per trial. Regardless of the number of conspecifics, or their body size, food was always monopolized by a single individual. In the case of two similar sized individuals, only one moved towards the food, while the other either disregarded the food (75%) or remained stationary (25%). In the case of two individuals of different sizes, both remained stationary in 75% of trials. In one instance, the larger individual approached the food while brushing along the immobile smaller individual with the edges of its arms before reaching the food and beginning to feed (~55 min of contact between individuals). When five individuals of various sizes were tested, food was monopolized by the first individual to reach it, regardless of its size. One exception was noticed when the smallest sea star reached the food first; a medium sized individual approached ~60 min later and partially overlapped its conspecific. The interaction lasted for 36 min until the small individual retreated, allowing the larger sea star free access to the food until the end of the trial (Supplementary Video S3.4). The

food was initially touched either with the podia at the tip of one arm or the inner sides of two arms. In the latter case, the two arms initially surrounded the food before the sea star moved on top of it.

In all treatments, individuals approached food in straight paths unless they encountered a conspecific, in which case they skirted around each other (Supplementary Video S3.5). Positive responses to the food occurred in 35.5 ± 11.3 min in trials involving two similar sized individuals, 58 min in the positive trial involving a pair of unequal size, and 50.0 ± 444.1 min in trials involving 5 individuals (Table 3.3). In the absence of a response to the food, or in the control trials, individuals either remained stationary or roamed around the tank (Table 3.4, Figure 3.2).

In trials involving similarly sized sea stars, no clear differences were detected for distance traveled ($F_{2,13} = 2.126$, $p = 0.159$), mean speed ($H_2 = 3.987$, $p = 0.159$), or maximum speed ($F_{2,13} = 2.468$, $p = 0.123$; Figure 3.2 A, B). In trials involving two differently sized sea stars, size was found to have a clear impact on absolute distance traveled ($F_{1,19} = 4.851$, $p = 0.044$) while response type did not ($F_{2,18} = 2.827$, $p = 0.091$) and there was no clear interaction between these two factors; large individuals in the control trials traveled significantly further than other large individuals, and large individuals overall traveled further than small ones (Figure 3.2 C). There was a clear interaction between body size and response type for mean speed ($F_{2,18} = 5.424$, $p = 0.017$); independent tests showed that response did not affect mean speed for either size class (small: $t = 0.099$, $p = 0.924$; large: $F_{2,5} = 2.574$, $p = 0.170$) but that mean speed was statistically different between size classes, with large individuals traveling faster than small ones ($t = 2.624$, $p = 0.02$; Figure 3.2 D). There was also an interaction between size and response type for maximum speed ($F_{2,18} = 3.93$, $p = 0.042$) and independent tests showed that response type did

not clearly affect maximum speed for either size class (small: $t = 0.491$, $p = 0.641$; large: $F_{2,5} = 1.769$, $p = 0.263$) but that, similar to mean speed, maximum speed statistically differed between size classes, with large individuals traveling faster ($t = 2.665$, $p = 0.019$; Figure 3.2 D).

3.4.3 Henricia lisa

When two individuals (no distinct size classes in this species) were tested together, they made contact through the podia at the tip of their arms in 50% of trials (1.0 ± 1.4 contacts per trial). Three of these contacts occurred in the same trial over a period of 20 min and lasted ≤9 min. In the three positive trials only one of the two individuals approached the food, so no clear monopolization behaviours were observed. When reaching the food, in 66% of all positive trials, individuals displayed "tapping" whereby the tip of an arm was successively applied to and lifted from the food (~1 min per tap, ≥ 3 taps per observation) with limited displacement of the arm tip (~1 cm per tap) over the food (Supplementary Video S3.6).

When approaching food, paths were either straight (33%) or curved (66%). In the former the arm closest to the food always led, whereas in the latter, a different arm led initially before the arm closest to the food took the lead (one leading arm change per trial, Supplementary Video S3.7). The response time of individuals approaching the food was 26.0 ± 22.5 min (Table 3.3), whereas individuals that disregarded the food and individuals in the control treatment roamed around the tank (Table 3.4, Figure 3.3).

In trials involving two individuals simultaneously, there were no clear differences between response types detected for distance traveled ($F_{2,13} = 0.333$, $p = 0.723$), mean speed ($F_{2,13} = 0.335$, $p = 0.722$) or maximum speed ($F_{2,13} = 0.306$, $p = 0.742$; Figure 3.3).

3.4.4 Buccinum scalariforme

Contact among paired conspecifics (no distinct size classes in this species) occurred only once across all four trials (0.3 ± 0.5 contacts per trial), wherein the siphon of one individual touched the shell of the other for less than 10 s. When an individual moved toward and contacted food (75% of trials, one individual per trial), the siphon made sweeping movements and remained pointed in the direction of the food item.

Paths toward the food were straight, either from the onset (66% of positive trials, Supplementary Video S3.8) or after moving haphazardly for ~45 min (33% of positive trials). The response time was 3.0 ± 22.8 min (Table 3.3). Individuals that disregarded the food, or that were in the control treatment, roamed around the tank (Table 3.4, Figure 3.4).

In trials involving two individuals at the same time, no clear differences were detected between response types for distance traveled ($F_{2,13} = 0.184$, $p = 0.834$), mean speed ($F_{2,13} = 0.986$, $p = 0.399$) or maximum speed ($F_{2,13} = 0.627$, $p = 0.550$; Figure 3.4).

3.4.5 C. granularis vs. H. lisa

When one individual each of *C. granularis* and *H. lisa* were tested together, contacts happened once in each of the short and prolonged duration trials. It involved the tips of the arms or the arm of *H. lisa* passing over immobile *C. granularis*, which displayed no visible avoidance behaviours (i.e. it did not move away, curl its arms, or retract terminal podia) in response to *H. lisa* touching it. Once at the food, *H. lisa* engaged in the tapping behaviour described previously in both prolonged duration replicates.

In short duration experiments neither species fed, with individuals traveling around the tank or remaining stationary rather than approaching the food, but *H. lisa* did travel further and

faster than *C. granularis* in both experimental and control treatments (Figure 3.5, A, B, Table 3.4). In prolonged trials, *H. lisa* approached food with direct, straight paths (100%), responding in 12.0 ± 8.5 min (Table 3.3) and fed in both trials. *C. granularis* did not feed in the prolonged duration experimental treatment, instead traveling around the tank or remaining immobile for long periods of time.

In short duration trials, distance traveled was clearly affected by species ($F_{1,14} = 18.584$, $p = 0.001$) and response type ($F_{1,14} = 7.705$, $p = 0.0168$) without any clear interaction between these factors; specifically, *H. lisa* in negative trials clearly traveled further than individuals in control trials (Figure 3.5 A). There was a clear interaction between species and response type for mean speed ($F_{1,14} = 6.968$, $p = 0.023$); independent tests showed no clear effect of response type on mean speed for *C. granularis* ($t = 1.191$, $p = 0.279$), while response type did affect the mean speed of *H. lisa*, with individuals in negative trials traveling faster than those in control trials ($t = 3.685$, $p = 0.010$). There was a difference between species, with *H. lisa* traveling more quickly than *C. granularis* ($t = 4.148$, $p = 0.001$; Figure 3.5 B). There was also a clear interaction between factors (species and response type) for maximum speed ($F_{1,14} = 5.914$, $p = 0.0316$) and independent tests showed that response type influenced the maximum speed of *H. lisa*, with individuals in negative trials traveling faster than those in control trials ($t = 2.499$, $p = 0.047$, but not *C. granularis* ($t = 0.418$, $p = 0.690$). Similar to mean speed, there was a clear difference in maximum speed between species, with *H. lisa* traveling fastest ($t = 4.54$, $p = 0.0005$; Figure 3.5 B).

3.4.6 C. granularis vs. B. scalariforme

When one individual each of *C. granularis* and *B. scalariforme* were released together contact/interaction only occurred once, during a short duration trial. In that instance, *B.*

scalariforme approached *C. granularis* and then crawled over it completely (this took 2 min and no reaction from *C. granularis* was noted; i.e. arm curling or moving away). In all other trials, where no direct interaction occurred, both individuals wandered around the tank.

In both short and prolonged trials, *B. scalariforme* did not approach the food, but it traveled over greater distances and faster than *C. granularis* (Figure 3.5, C, D, Table 3.4). *C. granularis* approached food in straight paths (100%) with the arm closest to the food acting as the leading arm and fed in 50% of short duration trials and in 100% of prolonged trials. The response time in the short duration experiment was 31.0 ± 17.0 min while the prolonged experiment response time was 17.5 ± 0.7 min (Table 3.3). Individuals of *C. granularis* that did not approach the food in short duration trials, or individuals in the control treatment, were either largely immobile or traveled short distances (Figure 3.5, C, D, Table 3.4).

Due to unequal datasets (*B. scalariforme* had no positive trials), two-way ANOVAs were not performed for this set of trials; instead a series of independent one-way ANOVAs and t-tests were performed to explore effects. Distance traveled was clearly different between species (t = 4.285, p = 0.0008), with *B. scalariforme* traveling further than *C. granularis*, whereas it was not clearly different between response types in either *C. granularis* ($F_{2,5}$ = 1.098, p = 0.403) or *B. scalariforme* (t = 0.611, p = 0.564; Figure 3.5 C). The two species also exhibited clearly differing mean speeds, with *B. scalariforme* moving faster (t = 4.751, p = 0.0003). Response type did not have a clear effect on the mean speed of *C. granularis* ($F_{2,5}$ = 0.822, p = 0.491) or *B. scalariforme* (t = 0.449, p = 0.669; Figure 3.5 D). Maximum speed was clearly different between the two species, with *B. scalariforme* moving most quickly (t = 6.578, p < 0.0001); however, neither *C. granularis* ($F_{2,5}$ = 0.916, p = 0.458) nor *B. scalariforme* (t = 0.467, p = 0.657) showed any clear change in maximum speeds between response types (Figure 3.5 D).

3.4.7 Mix of C. granularis, H. lisa, and B. scalariforme

When one individual each of *C. granularis*, *H. lisa*, and *B. scalariforme* were tested together, at least two of the three individuals made contact 2.3 ± 1.3 times per trial. In 75% of trials *B. scalariforme* crawled over the other individuals (both sea star species); this contact was brief (~2 min) and neither sea star species showed any visible reaction (i.e. moving away, arm curling, retraction of terminal podia). There was one instance of longer contact by *B. scalariforme* where it remained over the arm of *H. lisa* while both individuals were feeding (~4 h). *C. granularis* engaged in previously described wedging behaviour in 50% of trials, attempting to push itself under the arms of *H. lisa* or under the foot of *B. scalariforme* in order to reach food (Supplementary Video S3.9). Wedging was successful against *H. lisa*, which pulled its arms back and moved to a different location on the food when *C. granularis* pushed against and under it. Once *C. granularis* was established on the food, both species fed while still touching for the remainder of the trial. Wedging was met with mixed success against *B. scalariforme*. In one instance, *B. scalariforme* relocated to continue feeding, and in the other, *B. scalariforme* pushed back against *C. granularis*, forcing it to either only partially access the food or to move to an unoccupied area on the food.

All three species were attracted to the food during the trials, with differing frequencies. *H. lisa* approached food in a straight path (100% of positive trials) with the arm closest to the food becoming the leading arm. *H. lisa* was the first individual to reach food in 50% trials, fed in 75% of trials, and had a response time of 65.0 ± 145.2 min (Table 3.3). *B. scalariforme* typically approached food after traveling around the tank. However, once *B. scalariforme* began to approach food, the path was straight (100% of positive trials) with the siphon pointed towards the food. *B. scalariforme* approached food from both upstream and downstream directions; it

reached food first in 50% of trials, fed in 75% of trials, and had a mean response time of 103.0 ± 79.4 min (Table 3.3). *C. granularis* approached food in a straight path (100% of positive trials) with the arm closest to the food leading. *C. granularis* was never the first individual to reach food, fed in 75% of trials, and had a mean response time of 188.0 ± 341.7 min (Table 3.3).

3.4.8 Food falls

All four focal species were attracted to the salmon food fall. Based on visit scores over the course of the 12 days of observation, individuals of *C. granularis* fed upon the salmon carcass 21 times (1.8 ± 1.6 individuals day^{-1}), *H. phrygiana* fed 30 times (2.5 ± 2.3 individuals day^{-1}), *H. lisa* fed 20 times (1.7 ± 1.7 individuals day^{-1}) and *B. scalariforme* fed 5 times (0.4 ± 0.9 individuals day^{-1}, Figure 3.6 A). *C. granularis* visited the food fall more than *H. lisa* and *B. scalariforme* and no other clear differences were detected ($H_3 = 10.37$, $p = 0.016$; Figure 3.6 A). How many of these scores were of the same or different individuals cannot be determined. All three sea star species were observed occupying the salmon for periods of time greater than 24 h, while *B. scalariforme* typically only occupied the salmon in shorter bouts, ranging in length from a few minutes to a few hours (≤ 4 h). The main areas of food fall occupation for all species were the head, the exposed organs and flesh along the ventral surface, and the tail (see Supplementary Video S3.10).

An individual of *H. lisa* began to feed upon the exposed eye of the salmon within the first 2 days and remained there for almost 48 h (resisting attempts by another *H. lisa* and a small *H. phrygiana* to dislodge it). When the individual left, the eye appeared to be completely consumed, leaving an empty socket. An individual of *B. scalariforme* was observed to insert its head/siphon into the slightly gaping mouth of the salmon for over an hour. The largest individuals of *H. phrygiana* favoured the cut along the ventral surface of the salmon and remained in this area for

≥24 h, while smaller individuals fed on all parts of the salmon rather than congregate along the ventral cut. There were multiple instances where individuals of *C. granularis* were aggressed/agitated by the infaunal polychaetes residing in the mud around the food fall, with the polychaetes appearing to bite at *C. granularis*. One such polychaete was pulled out of its burrow while latching on to *C. granularis* as it retreated from the food fall (Supplementary Video S3.11). On one occasion, a large individual of *H. phrygiana* appeared to display agitation for an unknown reason while feeding, shifting around and waving its podia/arms through the water erratically (Supplementary Video S3.10). *H. lisa* displayed pulsing of the dorsal body wall while feeding at the head of the salmon, as was described in *C. granularis* and *H. phrygiana* previously (Supplementary Video S3.12). *H. lisa* also engaged occasionally in the 'tapping' behaviour against the carcass and sometimes against other nearby animals (Supplementary Video S3.13).

All four focal species were also attracted to the octopus head used as the second food fall. Over the 29 days of observation, *C. granularis* fed upon the carcass 41 times (1.4 ± 1.2 individuals day^{-1}), *H. phrygiana* fed 45 times (1.6 ± 1.6 individuals day^{-1}), *H. lisa* fed 76 times (2.6 ± 2.4 individuals day^{-1}) and *B. scalariforme* fed 20 times (0.7 ± 1.2 individuals day^{-1}, Figure 3.6 B). *C. granularis* visited the food fall more than *B. scalariforme* but no other clear differences were detected (H_3 = 14.978, p = 0.002; Figure 3.6 B). Again, these scores could be of the same or different individuals. As the octopus head used for this food fall was much smaller than the salmon, no distinct areas of food occupation were identified. However, like the salmon food fall, all three sea stars fed for periods of over 24 h while *B. scalariforme* fed anywhere from a few minutes to several hours (≤4 h) at a time. A large individual of *H. phrygiana* caused a smaller conspecific to retreat from the food fall by moving up to it while sweeping two of its arms towards it. The smaller individual made four unsuccessful attempts to approach the food.

By this point (day 17) the food fall had become small enough to be effectively monopolized by the larger individual of *H. phrygiana*; however, one individual of *H. lisa* was also feeding close by (Supplementary Video S3.14). An individual of *B. scalariforme* was feeding on the carcass when a conspecific arrived and flipped the first individual off the food so that it could take its place; shortly after this, the first individual returned and flipped the second off the carcass, resuming its original feeding position while the second individual relocated elsewhere on the carcass (Supplementary Video S3.15). There were multiple instances of small individuals (≤5 cm diameter) of *H. phrygiana* crawling onto the shell of *B. scalariforme*, causing it to become agitated and occasionally engage in flipping/escape behaviours (abandoning the food completely twice). There were also instances of large individuals of *H. phrygiana* moving towards and raising multiple arms in the direction of *B. scalariforme*, (both interactions shown in Supplementary Video S3.16). Conversely, while there were instances of *C. granularis* or *H. lisa* crawling over the shells of *B. scalariforme,* these interactions did not cause *B. scalariforme* to react (it continued to feed or move unperturbed), and the sea stars often rested on the shell (sometimes >1 h) before crawling away.

When comparing the two food falls, no clear differences in the number of individuals visiting the food fall were detected in any of the four focal species (*C. granularis*: $t = 0.757$, $p = 0.454$; *H. phrygiana*: $t = 1.512$, $p = 0.139$; *H. lisa*: $t = 1.241$, $p = 2.023$; *B. scalariforme*: $U = 193$, $p = 0.586$), indicating no preference for salmon or octopus carrion for either species (Figure 3.9 A, B).

3.5 Discussion

This study highlighted variable degrees and intensities of competitive dynamics between selected species that co-exist in the deep sea of the Northwest Atlantic, which were primarily

driven by a mix of species identity (conspecific vs. heterospecific), body size, and number of individuals involved. Interestingly, no consistent patterns emerged regarding the competitive advantage of body size (large vs. small) or taxonomy (asteroid vs. gastropod), hinting at more complex species-specific adaptations. Comparisons with Chapter 2 also revealed that two of the species responded differently to food based on the presence or absence of competitive pressure, one more quickly, the other more slowly, whereas the two other species did not appear to modify their response times on the basis of being alone or in a group.

Intraspecific responses of the sea star *C. granularis* were either size-based competitive interference or displacement, or cooperative social reorganization among smaller individuals, while all visible interspecific interactions appeared to be competitive. When conspecifics of different sizes were tested together, large individuals pushed smaller conspecifics off and excluded them from the food. However, smaller individuals (≤4 cm) on occasion engaged in interference behaviour, whereby one of them intercepted a larger conspecific (>6.5 cm) before it could reach the food, allowing multiple small individuals to reach the food first and to feed cooperatively (rearranging around the food in a manner that granted them all access). The apparent cooperation of smaller conspecifics to outcompete a larger conspecific, and multiple individuals actively rearranging so they can feed together, have not been explicitly reported before in sea stars. The rarity of food in the deep sea (Degen et al., 2015) may have enticed collaboration instead of competition among similarly sized conspecifics to ensure the density of individuals remained in the acceptable range for optimal social interaction, such as reproduction (Mercier & Hamel, 2009). In other words, cooperation could be exacerbated in some deep-water species compared to shallow-water counterparts that have access to a greater abundance of prey. Zemel and Lubin (1995) used ecological models to show that, when resources are scarce and

patchy, inter-group competition may outweigh within-group competition (with groups in the case of our study being specific-size classes) and encourage foraging in sub-optimal group sizes. Cronin and Snowdon (2008) found that even with unequal reward distributions, cooperative problem solving could persist in cotton top tamarins (*Saguinus oedipus*), even in cases where one participant received no rewards at all. The behaviours recorded here in *C. granularis* imply that size can be detected via physical contact and/or chemical communication, possibly through contact via the terminal podia. It is widely accepted that the terminal podia act as chemosensory structures in sea stars, even if the exact mechanism is unclear (Sloan, 1980; Sloan & Northway, 1982; Garm, 2017). It seems plausible that larger individuals, because they are more reproductively mature, emit different chemical cues than smaller individuals, allowing conspecifics to identify the general size (and level of threat) posed by another individual, and decide if they should cooperate or compete. Distinct chemical signatures based on the level of gametogenic maturity have been reported in other echinoderms, i.e. sea cucumbers (Hamel & Mercier, 1996). Moreover, some sea stars have the ability to identify conspecifics via chemosensory cues; i.e. in Y-maze tests, *Crossaster papposus* displayed avoidance behaviours towards the odor plumes of conspecifics (Sloan & Northway, 1982). Shallow-water sea star species are known to compete for food with other taxa occupying similar trophic levels (Menge, 1972; Ribi et al., 1977; Rogers et al., 2018). Unsurprisingly, when *C. granularis* was tested with other species, direct interactions were always of a competitive nature, and this was regardless of similar body sizes in the case of the sea star *H. lisa*. Findings from Stuckless et al. (in submission; see Chapter 2) and Gale et al. (2013) suggest that these sea star species both prey upon sponges, which could partly explain their competitive relationship. Antagonistic interactions between *C. granularis* and unidentified infaunal polychaetes in the mesocosm study

were observed where the latter appeared to pinch or bite individuals of *C. granularis* that approached their burrows near the food falls. The polychaetes were not observed to interact physically with any of the other focal species.

In contrast to *C. granularis*, *H. phrygiana* always displayed competitive behaviours towards conspecifics (i.e. directly pushing or sweeping arms towards smaller conspecifics), whereby an individual drove all others away from the food, to the point of monopolizing smaller items (e.g. solitary cup corals, pieces of octopus). Small individuals of *H. phrygiana* were easily chased off or pushed away from the food by larger conspecifics; maybe because unlike larger individuals they were unable to both engulf the food and maintain contact with the underlying substrate for stability. Among the focal species, this represented the only example of size-asymmetric competition, whereby larger individuals have a distinct competitive advantage over smaller ones (Nakayama & Fuiman, 2010). This type of interaction has been observed in sea stars before (Rogers et al., 2018). Of the three sea stars studied, *H. phrygiana* is also the only one with large pedicellariae (on both the oral and aboral surfaces; Mah et al., 2014). Pinching other individuals using the pedicellariae is a known interference behaviour in shallow-water sea stars (Gaymer et al., 2002; Rogers et al., 2018). The presence of such large pedicellariae may also explain why the individuals of *H. phrygiana* in this study never overlapped each other and were not actively crawled over by any of the other species during the frenzy created by the simulated food falls where all four focal species were present.

The sea star *H. lisa*, stood apart from the others in displaying very little direct interaction among conspecifics; their encounters might be described as neutral (e.g. brushing of arms). Since individuals of *H. lisa* were all of similar sizes, these results align with the findings of Rogers et al. (2018) where small conspecifics and heterospecifics of the sea stars *P. ochraceus* and *E.*

troschelii did not display interference behaviours towards each other. Alternately, this neutral behaviour among conspecifics may exist because *H. lisa* frequently feeds upon sponges (Robertson et al., 2017; Stuckless et al., in submission), which are typically large and sessile (i.e. plentiful and accessible; Beazley et al., 2013; 2015) and abundant in deep waters off the coast of Newfoundland (Murillo et al., 2012; Murillo et al., 2016); thus decreasing the need for competitive behaviours among feeding conspecifics. Notably, *H. lisa* was outcompeted by *C. granularis* in heterospecific trials involving chunks of octopus as the latter wedged under the former and pushed it away. During the food fall experiments *H. lisa* fed upon the exposed eye of the salmon and around its mouth, perhaps favouring the softer, scale-less tissues, and also exhibited pulsing of the dorsal body wall similar to what has been described in *C. granularis* and *H. phrygiana* in previous studies (Gale et al., 2013; Stuckless et al., in submission)

Interactions between conspecifics of the gastropod *B. scalariforme* were infrequent and neutral during the trials. However, in the food fall experiments, interactions of a competitive nature between conspecifics were seen, with individuals flipping/pushing each other off the food, even when there was ample space to accommodate multiple individuals, evoking competition for favoured locations on the food. Feeding on tissue patches tenderized by the efforts of another *B. scalariforme* may require less energy, justifying such interaction between conspecifics. Similarly, Brown and Alexander Jr (1994) found that individuals of the marine gastropod *Stramonita haemastoma* that approached and fed on oysters already weakened by conspecifics received more benefits (e.g. less energy expenditure) than the individual that initially broke through oyster shells. Interactions between *H. phrygiana* and *B. scalariforme* also appeared to be competitive during the food fall simulation. Individuals of *B. scalariforme* approached feeding individuals of *H. phrygiana* and were chased away by the larger sea stars or crawled over by

smaller sea stars. Both scenarios induced a flipping escape response typical of many other gastropod species (Watson et al., 2014). In a previous study, Stuckless et al. (in submission) found that *H. phrygiana* fed on deep-sea gastropod remains. Here, large individuals of *H. phrygiana* approached *B. scalariforme* with their arms raised off the substrate. Sloan and Northway (1982) described a similar lunging posture in *C. papposus* that detected prey cues. Shallow-water members of the *Buccinum* genus are often predated upon by sea stars (Thomas & Himmelman, 1988; Rochette et al., 1995; Rochette et al., 2001) and it seems likely based on the present results and those of Stuckless et al. (in submission) that *B. scalariforme* may also be preyed upon by large sea stars. Shallow-water members of the *Buccinum* genus have been reported to engage in kleptoparasitic behaviours with large predatory sea stars (Morissette & Himmelman, 2000; Rochette et al., 2001); a similar relation may exist between *B. scalariforme* and *H. phrygiana* in deep waters. As these two species are among the most common at bathyal depths off the coast of eastern Canada, and they are often collected simultaneously (J-F Hamel, personal observations), it is not impossible that competition for the same resources has developed between the two.

Comparing the present results to those of Stuckless et al. (in submission; see Chapter 2), who studied the same species individually, revealed that the mean time required by *C. granularis* to reach the food remained roughly consistent, with the exception of trials involving *C. granularis*, *H. lisa*, and *B. scalariforme* together, which showed longer mean response times. Published work suggests that *C. granularis* is an opportunistic generalist (Gale et al., 2013; Stuckless et al., in submission), which may explain why this species responds to food cues consistently across most situations, whether competition is present or not. However, in singleton trials with *H. phrygiana*, Stuckless et al. (in submission) recorded a wide variation in response

times that was driven by differing food stimuli, suggesting a wider diet spectrum for that species, as supported by Gale et al. (2013). Consistent reaction times were obtained here in trials with many individuals offered the same food (the cup coral *F. alabastrum*), suggesting that the food type is the main driving factor. In contrast, *H. lisa* responded more quickly when multiple individuals were present (conspecifics or otherwise) than when tested alone. In half of the singleton trials, *H. lisa* travelled in large loops when approaching food (Stuckless et al., in submission); whereas in the present study involving multiple individuals, a straighter path to the food was consistently detected, hinting either at increased haste or better detection. It was speculated that the cross-current loops may have allowed *H. lisa* to sample more odor plumes (e.g. size and condition of food source), similar to the cross-current movement of some shallow-water sea stars (Rochette et al., 1994; Drolet & Himmelman, 2004). Perhaps *H. lisa* does not take the time to engage in pre-feeding assessment when other animals (conspecifics or heterospecifics) are present, due to competitive pressure. In support of this hypothesis, St-Pierre et al. (2018) found that the sea star *A. rubens* alters its foraging strategy when crabs are present in order to prioritize active feeding. Alternatively, gregarious foraging may heighten the detection capacity of *H. lisa*, yielding faster response times, perhaps via detection of chemical cues emitted into the water column during feeding (digestive fluids or damaged prey scent). The fourth species, the gastropod *B. scalariforme*, responded more slowly on average in the presence of multiple individuals than when alone (Stuckless et al., in submission). Two strategies were observed in this species: an individual directly approaching food from the trial onset (resulting in short response times) or approaching food in a straight line after traveling around the tank (resulting in long response times). A blend of these tactics was often observed across replicate trials, suggesting that the identity or presence of other individuals (conspecific or otherwise) may

not be the determining factor, and that the method of approaching food depicts behavioural plasticity. The latter has been described in many other marine gastropod species in regard to various stimuli, such as type of bait (Ilano et al., 2005), predator presence (Delgado et al., 2002), water acidity (Amaral et al., 2014), and wave action (Márquez et al., 2015).

Morphology, and related locomotor capacity, may provide some explanation for the different interactions observed. Stuckless et al. (in submission) determined that *C. granularis* is the slowest moving of the four focal species, perhaps from the combination of completely webbed arms and limited number of ambulacral podia compared to the other two sea star species (~20% vs. 25-29% coverage, Supplementary Table S3.1). On the other hand, the webbed arms may be beneficial to *C. granularis* from scavenging or competitive perspectives as they may enable the wedging strategy discussed earlier, removing the need to reach the food quickly. Webbed arms may represent a morphological trade-off for this species, i.e. slower movement speed for greater ability to actively compete for space at a feeding site. Morphological trade-offs are present in other groups such as gastropods (Delgado et al., 2002), mussels (Addison, 2009), fishes (Ferry-Graham et al., 2002), many species within the mammalian order Carnivora (Van Valkenburgh, 2007), and species that live in darkened environments like caves or the deep sea (Sumner-Rooney, 2018). The long, narrow arms of *H. lisa*, by comparison, have higher podia coverage than the other two sea star species (~29% vs. 20-25% coverage, Supplementary Table S3.1), which may explain the proportionally high speeds achieved by this species for its size, as measured in Stuckless et al. (in submission). These thin, flexible arms could be advantageous when feeding upon the uneven and perforated surface of sponges that constitute common food sources for the *Henricia* genus (Sheild & Witman, 1993; Robertson et al., 2017; Stuckless et al., in submission). However, such arms seem poorly suited to repulsing competitors or tightly

gripping more even surfaces, leaving them vulnerable to the wedging tactics of *C. granularis* on smoother foods (e.g. small chunks of octopus). The gastropod *B. scalariforme* is the fastest of the focal species (Stuckless et al., in submission), and the muscular foot appears to give it a means of resisting the wedging tactics of *C. granularis*. Other species of *Buccinum* have been observed to successfully compete with a wide variety of taxa for food resources, including sea stars, crabs, and fishes (Morissette & Himmelman, 2000; Rochette et al., 2001; Aguzzi et al., 2012).

During the two food fall experiments, *H. phrygiana* consistently reached the food first, perhaps due to its high speed compared to the other sea star species and because *B. scalariforme* does not always directly approach food items (Stuckless et al., in submission). On the salmon remains, the softer tissues of the eye and mouth appeared to be favoured by the focal species along with the cut along the ventral surface that exposed the internal organs. These softer scale-less tissues may be easier for the focal species to consume, given the absence of predators (e.g. fishes, crustaceans) observed around food falls *in situ* (Klages et al., 2000; Premke et al., 2006; Higgs et al., 2014) that normally open or tear the flesh. On the octopus, no areas of preference were identified, perhaps because it was smaller in size or because it lacked scales or hard parts. All the focal sea star species fed on the food falls for over 24 h whereas *B. scalariforme* only fed in short bouts (<4 h) similar to reports in other whelks (Evans et al., 1996; Ilano et al., 2005). The only non-focal species that overtly interacted with the food fall and focal species were the unidentified infaunal polychaetes that lived in the mud around the food fall. They were observed attacking and biting individuals of *C. granularis* that neared their burrows and feeding on the food falls themselves. The polychaetes may have only interacted with the *C. granularis* due to their slower speed, which left them vulnerable to attack, and/or small size. Some sea stars and gastropods are known to prey upon polychaetes (Dearborn et al., 1991; Evans et al., 1996; Ilano

et al., 2005), thus the other focal species may have been predators. The brittle stars in the mesocosm were observed on the sediment around the food falls, sometimes gathering in large numbers, but did not climb on the food fall or impede the behaviour or movement of the focal species. Likewise, the single individual of *C. papposus* in the mesocosm at times moved close to the food falls but was never observed directly engaging with them or with the focal species.

The present study shows that competitive behaviours and dynamics in co-existing benthic animals from the deep sea vary depending on species identity and the size/number of the individuals involved. The initial hypothesis that larger individuals would always outcompete smaller individuals was not verified, as exemplified by the cooperative interference behaviour among small/medium individuals of *C. granularis* against larger conspecifics. Likewise, the hypothesis that faster species would outcompete slower species was not verified, as the slowest species in this study (*C. granularis*) was able to outcompete faster species of a similar size (*H. lisa* and *B. scalariforme*) in competitive scavenging settings, presumably thanks to its morphological adaptation and wedging strategy. Understanding how animals interact with others in their environment (conspecifics or otherwise) provides insights into potential dominance hierarchies and competitive dynamics (Menge, 1972; Schmid & Schaerer, 1981; Schmitt, 1987; Sbragaglia et al., 2017; Majer et al., 2018). As resource exploitation and other anthropogenic pressures in the deep sea are likely to increase in the future, understanding how currently understudied deep-water ecosystems function, and how the species within them interact, should allow us to better protect these unique areas and species (Ramirez-Llodra et al., 2011; Danovaro et al., 2014; Mestre et al., 2014; Levin & Le Bris, 2015).

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3.8 Tables and Figures.

Table 3.1 Size classes and mean sizes (± SD) of focal species used in different experimental treatments.

Species	Size Class	Diameter/Shell length (cm)	Treatments (duration)
Ceramaster granularis	Small	3.7 ± 0.2	Two *Ceramaster* different sizes (short) Five *Ceramaster* (prolonged)
	Medium	4.7 ± 1.1	Two *Ceramaster* same size (short) Five *Ceramaster* (prolonged) *Ceramaster* and *Henricia* (short/prolonged) *Ceramaster* and *Buccinum* (short/prolonged) *Ceramaster*, *Henricia*, and *Buccinum* (prolonged)
	Large	6.9 ± 0.2	Two *Ceramaster* different sizes (short) Five *Ceramaster* (prolonged)
Hippasteria phrygiana	Small	11.9 ± 0.3	Two *Hippasteria* different sizes (short) Five *Hippasteria* (prolonged)
	Medium	15.3 ± 2.3	Two *Hippasteria* same size (short) Five *Hippasteria* (prolonged)
	Large	17.9 ± 1.3	Two *Hippasteria* different sizes (short) Five *Hippasteria* (prolonged)
Henricia lisa	N/A	5.3 ± 1.0	Two *Henricia* (short) *Ceramaster* and *Henricia* (short/prolonged) *Ceramaster*, *Henricia*, and *Buccinum* (prolonged)
Buccinum scalariforme	N/A	6.5 ± 0.7	Two *Buccinum* (short) *Ceramaster* and *Buccinum* (short/prolonged) *Ceramaster*, *Henricia*, and *Buccinum* (prolonged)

Table 3.2 Mean ratio of total body wet weight to food weight (± SD) for individuals of the different species that responded positively to the food.

Species	Treatment*	Animal Weight per g of Food (g ± SD)
Ceramaster granularis	Two same sized	1.0 ± 0.1
	Two differently sized	1.5 ± 0.2
	Five differently sized	2.7 ± 0.4
	Ceramaster and *Buccinum* (short)	3.2 ± 0.0
	Ceramaster and *Buccinum* (prolonged)	3.4 ± 0.3
	Ceramaster, *Henricia*, and *Buccinum* (prolonged)	3.7 ± 0.8
	All positive trials combined	**2.6 ± 1.1**
Hippasteria phrygiana	Two same sized	35.2 ± 3.9
	Two differently sized	22.6
	Five differently sized	72.9 ± 10.8
	All positive trials combined	**43.6 ± 26.2**
Henricia lisa	Two same sized	0.4 ± 0.0
	Ceramaster and *Henricia* (prolonged)	1.0 ± 0.2
	Ceramaster, *Henricia*, and *Buccinum* (prolonged)	3.5 ± 0.9
	All positive trials combined	**1.6 ± 1.6**
Buccinum scalariforme	Two same sized	5.0 ± 0.7
	Ceramaster, *Henricia*, and *Buccinum* (prolonged)	3.7 ± 0.8
	All positive trial types combined	**4.3 ± 1.0**

*Treatment types that resulted in no response toward the food for a given species were omitted from the table for that species.

Table 3.3 Median response time (time to reach food ± SD) and mean response time (± SD, with and without outliers) for each species and treatment combination.

Species	Treatment*	Median Response Time (min ± SD)	Mean Response Time (min ± SD)	Mean Response Time Outliers Removed (min ± SD)
Ceramaster granularis	Two same sized individuals	21.0 ± 10.0	31.3 ± 10.0	
	Two differently sized individuals	40.0 ± 8.3	37.3 ± 8.3	
	Five differently sized individuals	45.0 ± 150.8	94.8 ± 150.8	51.3 ± 46.2
	C. granularis and *B. scalariforme* (short)	31.0 ± 17.0	31.0 ± 17.0	
	C. granularis and *B. scalariforme* (long)	17.5 ± 0.7	17.5 ± 0.7	
	C. granularis, *H. lisa*, and *B. scalariforme*	188.0 ± 341.7	294.7 ± 341.7	103.5 ± 119.5
	Across all treatments	**39.0 ± 161.7**	**90.4 ± 161.7**	**45.8 ± 44.9**
Hippasteria phrygiana	Two same sized individuals	35.5 ± 11.3	37.0 ± 11.3	
	Two differently sized individuals	58.0	58.0	
	Five differently sized individuals	50.0 ± 444.1	260.8 ± 444.1	34.7 ± 13.8
	Across all treatments	**45.5 ± 318.0**	**151.0 ± 318.0**	**38.8 ± 12.9**
Henricia lisa	Two same sized individuals	26.0 ± 22.5	27.0 ± 22.5	
	C. granularis and *H. lisa* (long)	12.0 ± 8.5	12.0 ± 8.5	
	C. granularis, *H. lisa*, and *B. scalariforme*	65 ± 145.2	117.0 ± 145.2	35.0 ± 42.4
	Across all treatments	**22.0 ± 93.2**	**57.0 ± 93.2**	**25.0 ± 24.0**
Buccinum scalariforme	Two same sized individuals	3.0 ± 22.8	15.7 ± 22.8	
	C. granularis, *H. lisa*, and *B. scalariforme*	103.0 ± 79.4	122.7 ± 79.4	
	Across all treatments	**48.5 ± 78.5**	**69.2 ± 78.5**	

*Treatment types that resulted in no response toward the food for a given species were omitted from the table for that species.

Table 3.4 Size classes used for each species in short duration treatments with distance traveled, mean speed, and maximum speed provided as mean ± SD for positive, negative, and control trials.

Species	Treatment (Food)	Size Class	Variable	Score*	Value (n)
Ceramaster granularis	Same size (Octopus)	N/A	Distance (cm)	Positive	9.0 ± 5.2 (4)
				Negative	6.1 ± 5.4 (4)
				Control	5.8 ± 3.2 (8)
			Mean Speed (cm min^{-1})	Positive	0.2 ± 0.1 (4)
				Negative	0.1 ± 0.1 (4)
				Control	0.1 ± 0.1 (8)
			Maximum Speed (cm min^{-1})	Positive	0.9 ± 0.5 (4)
				Negative	0.6 ± 0.4 (4)
				Control	0.8 ± 0.2 (8)
	Different sizes (Octopus)	Small	Distance (cm)	Positive	5.3 ± 2.5 (2)
				Negative	0.6 ± 0.6 (2)
				Control	1.4 ± 1.5 (4)
			Mean Speed (cm min^{-1})	Positive	0.1 ± 0.0 (2)
				Negative	0.0 ± 0.0 (2)
				Control	0.0 ± 0.0 (4)
			Maximum Speed (cm min^{-1})	Positive	0.6 ± 0.1 (2)
				Negative	0.3 ± 0.1 (2)
				Control	0.3 ± 0.1 (4)
		Large	Distance (cm)	Positive	7.6 (1)
				Negative	0.1 ± 0.1 (3)
				Control	1.5 ± 2.1 (4)
			Mean Speed (cm min^{-1})	Positive	0.2 (1)
				Negative	0.0 ± 0.0 (3)
				Control	0.0 ± 0.1 (4)
			Maximum Speed (cm min^{-1})	Positive	0.8 (1)
				Negative	0.1 ± 0.1 (3)
				Control	0.2 ± 0.2 (4)
Hippasteria phrygiana	Same size (Cup coral)	N/A	Distance (cm)	Positive	22.7 ± 4.2 (4)
				Negative	20.1 ± 13.6 (4)
				Control	10.5 ± 11.2 (8)
			Mean Speed (cm min^{-1})	Positive	0.4 ± 0.0 (4)
				Negative	0.3 ± 0.2 (4)
				Control	0.2 ± 0.2 (8)
			Maximum Speed (cm min^{-1})	Positive	1.3 ± 0.2 (4)
				Negative	1.2 ± 0.4 (4)
				Control	0.8 ± 0.5 (8)
	Different sizes (Cup coral)	Small	Distance (cm)	Positive	(0)
				Negative	1.4 ± 1.3 (4)
				Control	1.1 ± 2.0 (4)
			Mean Speed	Positive	(0)

			(cm min^{-1})	Negative	0.0 ± 0.0 (4)
				Control	0.0 ± 0.1 (4)
			Maximum Speed	Positive	(0)
			(cm min^{-1})	Negative	0.4 ± 0.1 (4)
				Control	0.3 ± 0.3(4)
		Large	Distance	Positive	14.9 (1)
			(cm)	Negative	2.3 ± 1.6 (3)
				Control	16.6 ± 12.0 (4)
			Mean Speed	Positive	0.2 (1)
			(cm min^{-1})	Negative	0.1 ± 0.1 (3)
				Control	0.4 ± 0.2 (4)
			Maximum Speed	Positive	1.1 (1)
			(cm min^{-1})	Negative	0.5 ± 0.3 (3)
				Control	1.4 ± 0.8 (4)
Henricia lisa	Two individuals (Sponge)	N/A	Distance	Positive	9.5 ± 5.3 (3)
			(cm)	Negative	14.0 ± 11.3 (5)
				Control	14.8 ± 9.5 (8)
			Mean Speed	Positive	0.2 ± 0.0 (3)
			(cm min^{-1})	Negative	0.3 ± 0.2 (5)
				Control	0.3 ± 0.2 (8)
			Maximum Speed	Positive	0.8 ± 0.2 (3)
			(cm min^{-1})	Negative	1.0 ± 0.4 (5)
				Control	0.8 ± 0.3 (8)
Buccinum scalariforme	Two individuals (Octopus)	N/A	Distance	Positive	67.5 ± 105.2 (3)
			(cm)	Negative	104.3 ± 82.0 (5)
				Control	84.7 ± 80.9 (8)
			Mean Speed	Positive	1.6 ± 1.5 (3)
			(cm min^{-1})	Negative	3.2 ± 1.5 (5)
				Control	3.4 ± 3.0 (8)
			Maximum Speed	Positive	6.0 ± 4.6 (3)
			(cm min^{-1})	Negative	9.6 ± 1.1 (5)
				Control	8.5 ± 4.0 (8)
Ceramaster granularis + *Henricia lisa*	One individual of each (Sponge)	Medium (*C. granularis*)	Distance	Positive	(0)
			(cm)	Negative	10.2 ± 5.8 (4)
				Control	6.4 ± 4.5 (4)
			Mean Speed	Positive	(0)
			(cm min^{-1})	Negative	0.2 ± 0.1 (4)
				Control	0.1 ± 0.1 (4)
			Maximum Speed	Positive	(0)
			(cm min^{-1})	Negative	0.7 ± 0.2 (4)
				Control	0.7 ± 0.2 (4)
		N/A (*H. lisa*)	Distance	Positive	(0)
			(cm)	Negative	42.1 ± 17.8 (4)
				Control	18.0 ± 6.1 (4)
			Mean Speed	Positive	(0)
			(cm min^{-1})	Negative	0.7 ± 0.2 (4)

				Control	0.3 ± 0.1 (4)
			Maximum Speed (cm min^{-1})	Positive	(0)
				Negative	2.2 ± 0.6 (4)
				Control	1.3 ± 0.3 (4)
Ceramaster granularis + *Buccinum scalariforme*	One individual of each (Octopus)	Medium (*C. granularis*)	Distance (cm)	Positive	10.5 ± 2.6 (2)
				Negative	28.7 ± 30.0 (2)
				Control	12.8 ± 4.4 (4)
			Mean Speed (cm min^{-1})	Positive	0.2 ± 0.1 (2)
				Negative	0.5 ± 0.5 (2)
				Control	0.2 ± 0.1 (4)
			Maximum Speed (cm min^{-1})	Positive	0.8 ± 0.1 (2)
				Negative	1.7 ± 1.4 (2)
				Control	1.3 ± 0.4 (4)
		N/A (*B. scalariforme*)	Distance (cm)	Positive	(0)
				Negative	190.1 ± 72.1 (4)
				Control	145.3 ± 127.9 (4)
			Mean Speed (cm min^{-1})	Positive	(0)
				Negative	3.5 ± 0.8 (4)
				Control	2.9 ± 2.4 (4)
			Maximum Speed (cm min^{-1})	Positive	(0)
				Negative	12.3 ± 2.1 (4)
				Control	10.8 ± 6.2 (4)

*Positive trials resulted in feeding, negative trials did not result in feeding, all control trials were pooled.

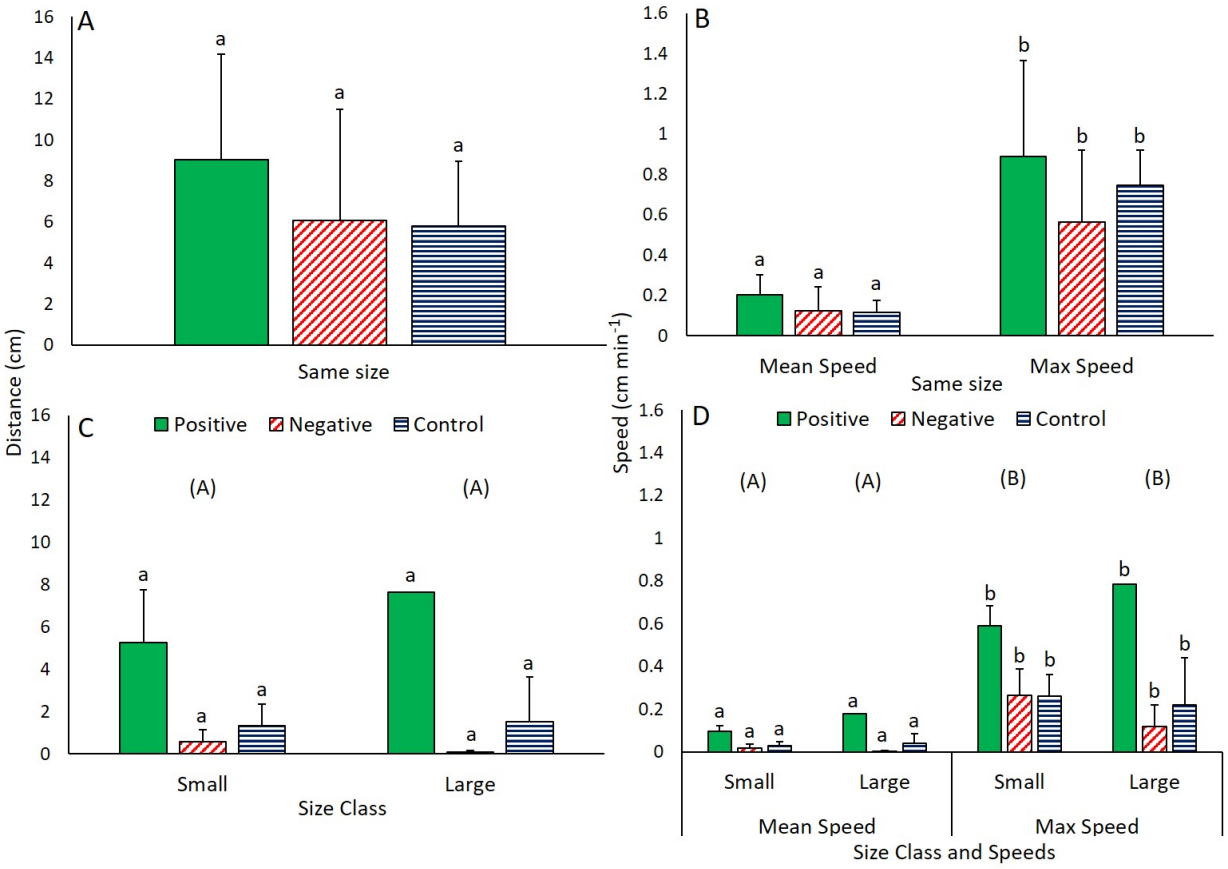

Figure 3.1 Mean distance traveled and mean and maximum speeds of *Ceramaster granularis* when two similarly sized individuals were tested (A & B) and when two differently sized individuals were tested (C & D). Data are provided as means ± SD where applicable. Means were compared between response types in one-way ANOVA with post-hoc Tukey test ($p < 0.05$ significance value) in A and B. Means were compared between sizes for each metric in C and D using two-way ANOVA with post-hoc Tukey test ($p < 0.05$ significance value). Bars with different letters are significantly different and groups with different letters are significantly different (within the same metric). See text for full results.

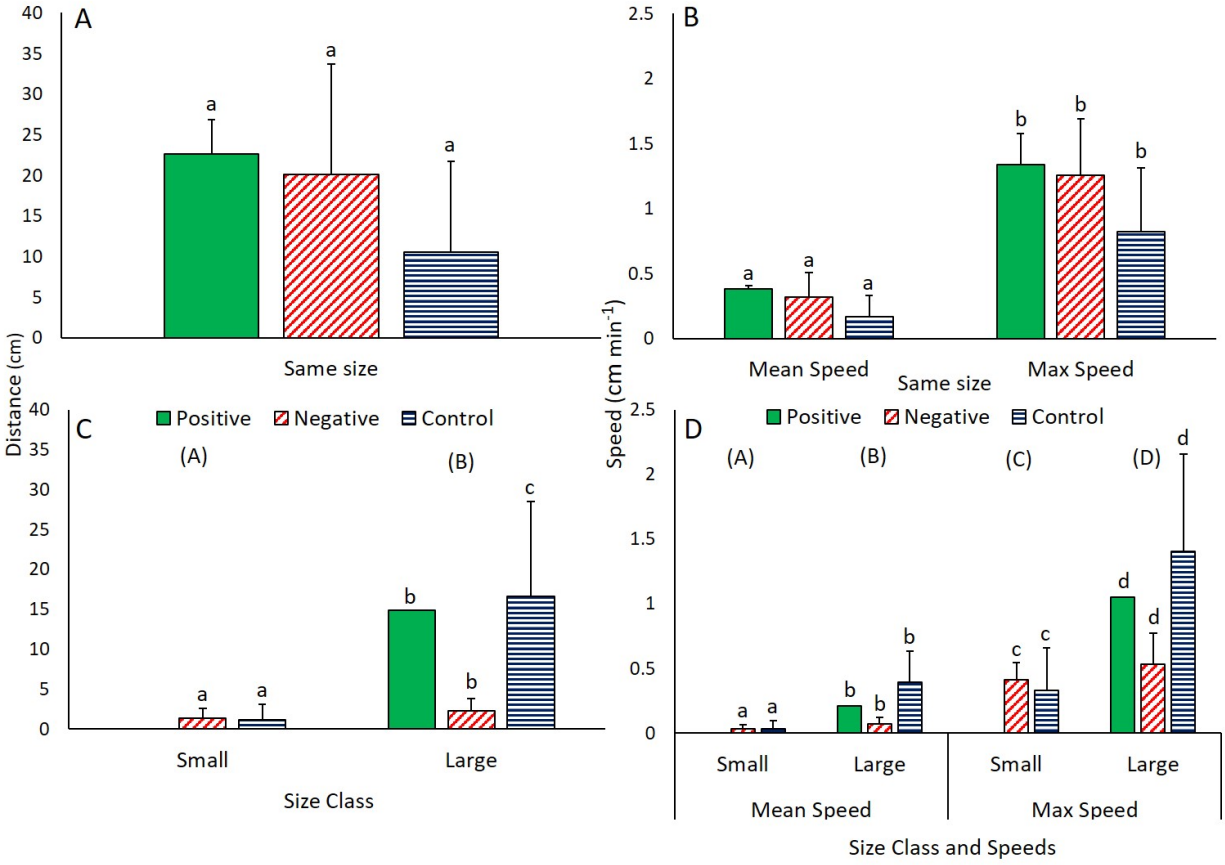

Figure 3.2 Mean distance traveled and mean and maximum speeds of *Hippasteria phrygiana* when two similarly sized individuals were tested (A & B) and when two differently sized individuals were tested (C & D). Data are provided as means ± SD where applicable. Means were compared between response types in one-way ANOVA with post-hoc Tukey test ($p < 0.05$ significance value) in A and B. Means were compared between sizes for each metric in C and D using two-way ANOVA with post-hoc Tukey test ($p < 0.05$ significance value). Bars with different letters are significantly different and groups with different letters are significantly different (within the same metric). See text for full results.

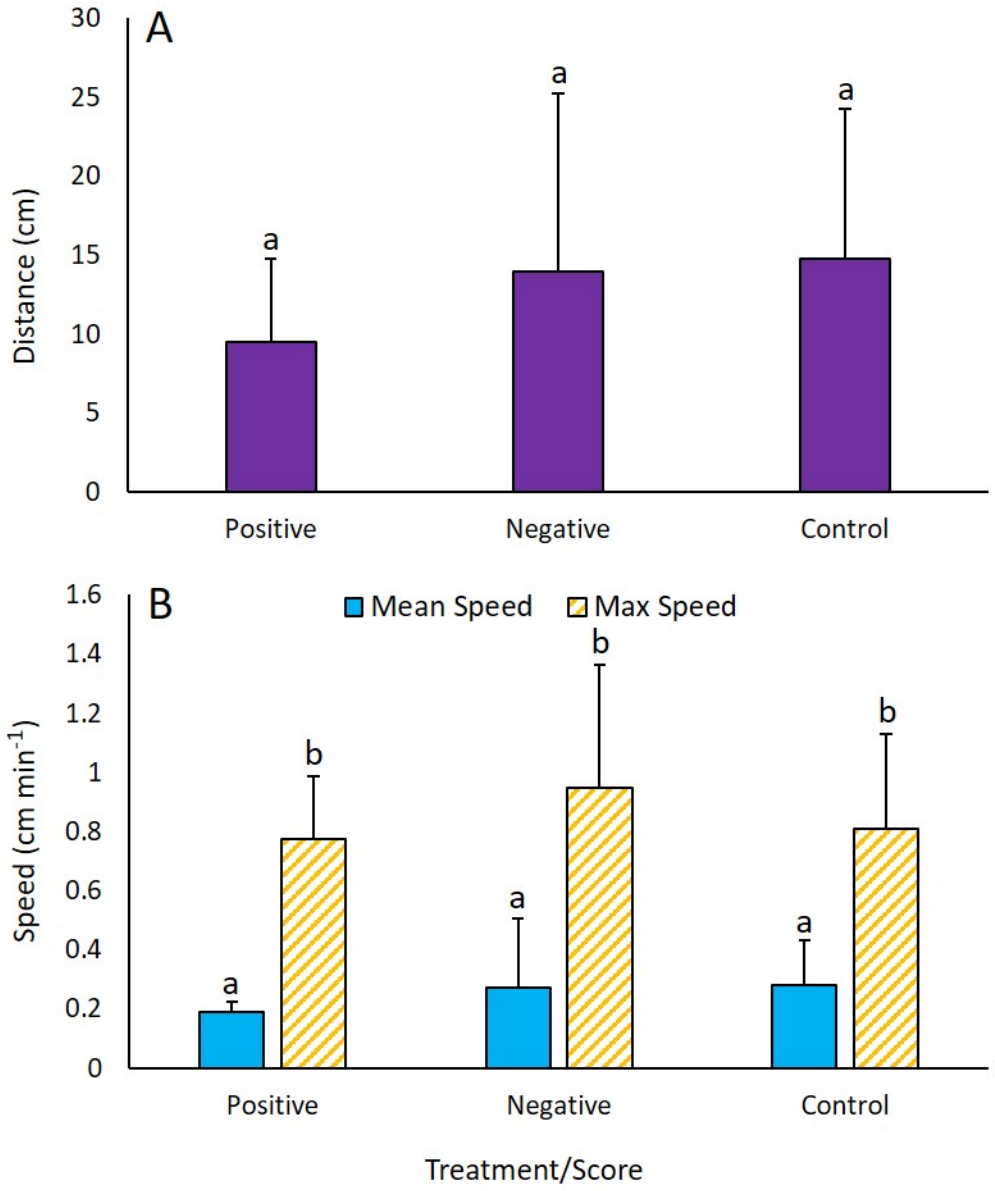

Figure 3.3 Mean distance traveled (A) and mean and maximum speeds (B) of *Henricia lisa* when two individuals were tested concurrently. Data are shown as mean ± SD. Means were tested across different response types for each metric using one-way ANOVA with post-hoc Tukey test (significance value of $p < 0.05$). Bars with different letters are significantly different from each other (for a given metric). See text for full results.

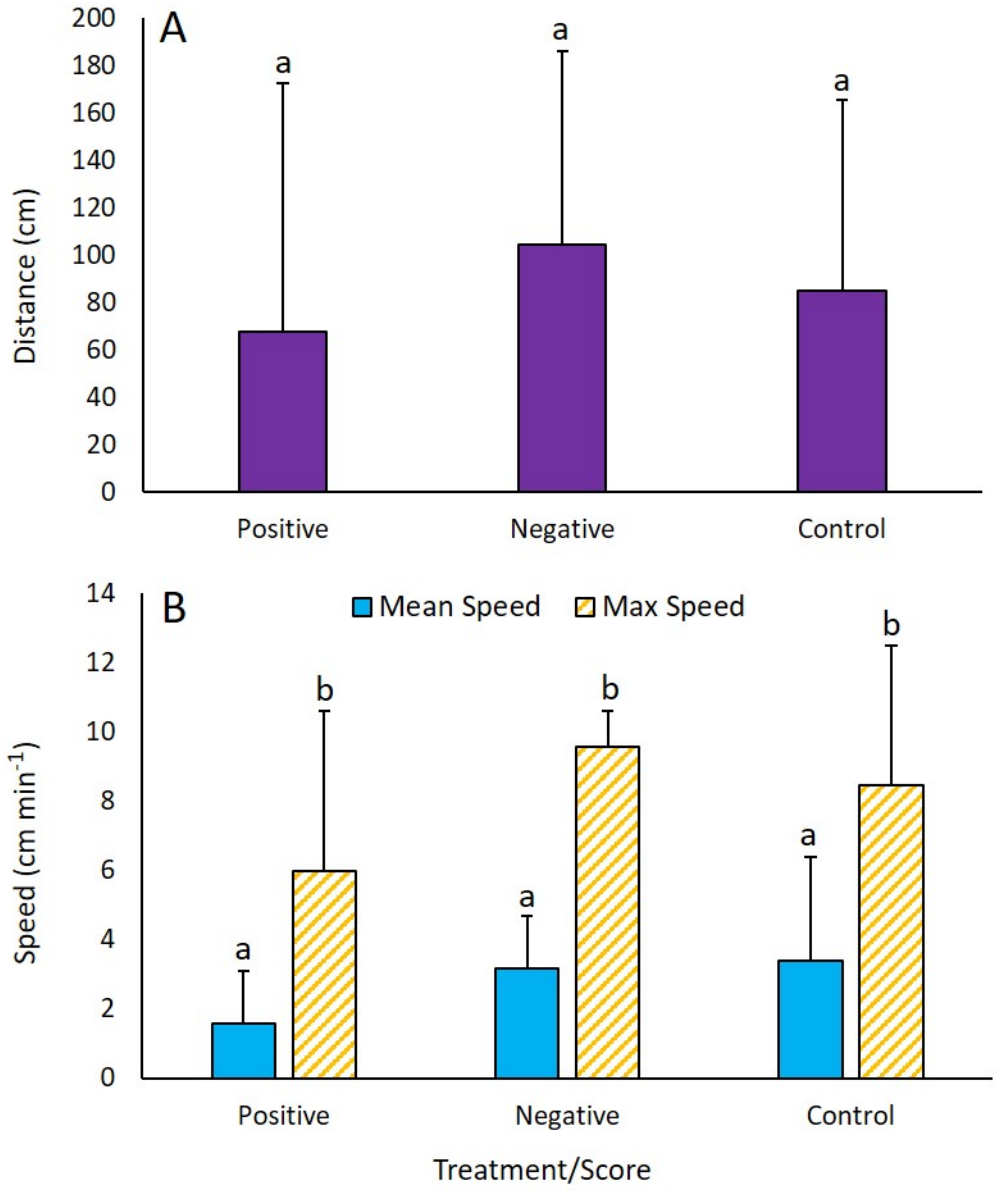

Figure 3.4 Mean distance traveled (A) and mean and maximum speeds (B) of *Buccinum scalariforme* when two individuals were tested concurrently. Data are shown as mean ± SD. Means were tested across different response types for each metric using one-way ANOVA with post-hoc Tukey test (significance value of $p < 0.05$). Bars with different letters are significantly different from each other (for a given metric). See text for full results.

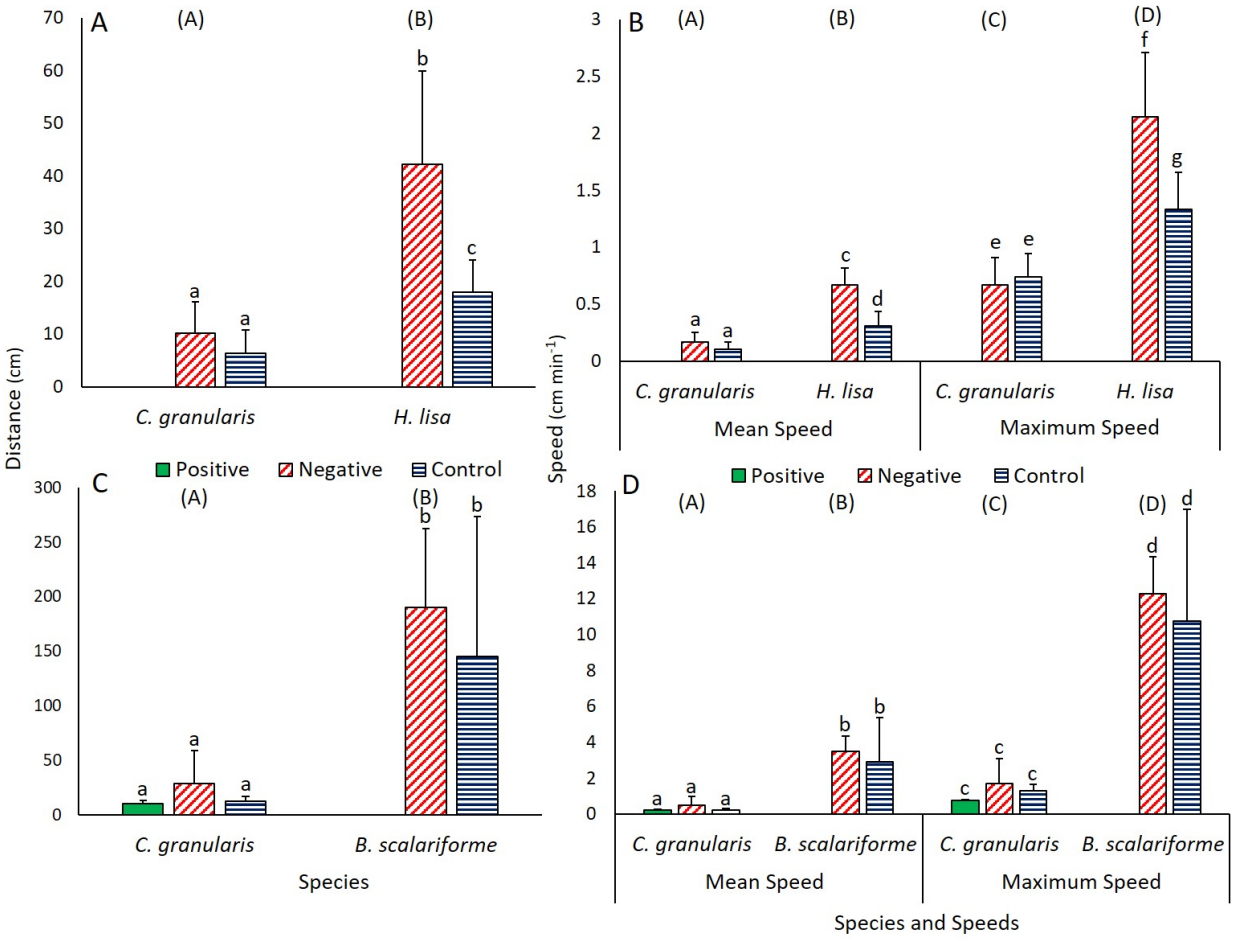

Figure 3.5 Mean distance traveled and mean and maximum speeds for *Ceramaster granularis* and *Henricia lisa* tested concurrently (A & B) and *C. granularis* and *Buccinum scalariforme* tested concurrently (C & D) in short duration trials. Please note different Y-axis scales for A & B, and C & D. Data are shown as mean ± SD. Means were tested within species and between species using two-way ANOVA in panels A and B and one-way ANOVA with post-hoc Tukey tests and t-tests for each factor as appropriate in panels C & D due to *B. scalariforme* having no positive trials. Bars with different letters are significantly different within a species for a given metric while groups with different letters are significantly different between species. See text for full results.

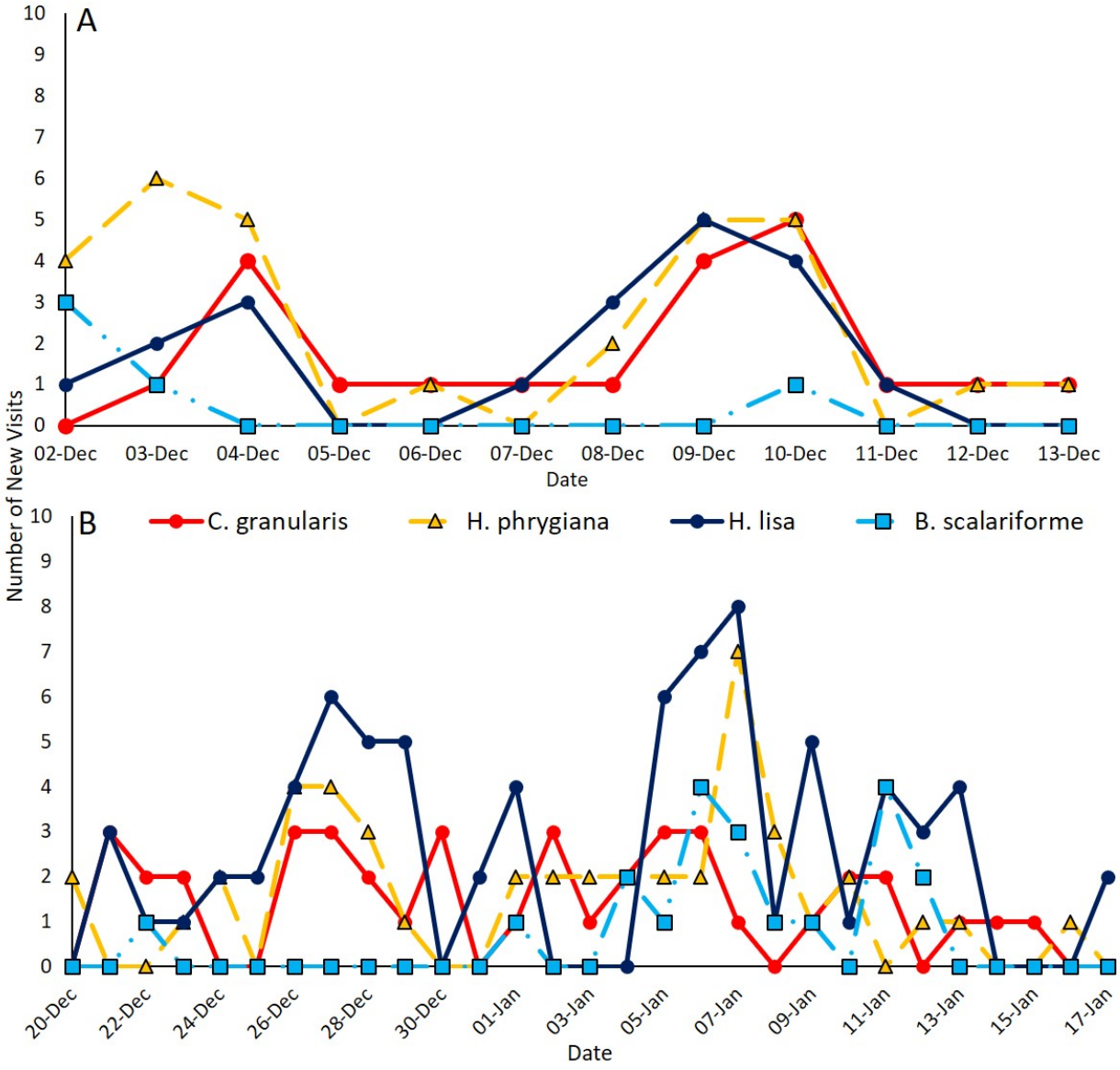

Figure 3.6 Number of independent visits scored for *Ceramaster granularis, Hippasteria phrygiana, Henricia lisa*, and *Buccinum scalariforme* to the (A) salmon fall, and (B) octopus fall, each day the fall was monitored. Means for each food fall were compared between species for each food fall type using a Kruskal-Wallis Test with post-hoc Dunn's tests (significance value $p < 0.05$). Means for each food fall type for each species were compared using an unpaired two-tailed t-test for parametric data or a Mann-Whitney test for non-parametric data (see text for full results).

3.9 Supplementary Material

3.9.1 Supplementary Tables

Table S 3.1 Approximate percentage of total oral surface covered by podia for each sea star species as determined through photo analysis in ImageJ

Species	Surface Covered by Podia (Mean% ± SD)
Ceramaster granularis	19.6 ± 2.3
Hippasteria phrygiana	25.4 ± 0.9
Henricia lisa	28.5 ± 4.6

Table S 3.2 Behaviour category results (in % of total time ± SD) for prolonged duration (18-23 h) trials for each species and size class, one measurement per hour for each trial (see text for description of behaviour categories).

Species	Food	Size/Species (n)	Behaviour	Treatment	% of Time (± SD)
Ceramaster granularis	Octopus	Small (4)	Immobile	Experimental	28.2 ± 35.2
				Control	14.9 ± 17.2
			Mobile	Experimental	21.4 ± 22.2
				Control	39.9 ± 29.6
			Contact Animal	Experimental	1.3 ± 2.5
				Control	2.3 ± 4.6
			Contact Stimulus	Experimental	0 ± 0
				Control	27.1 ± 45.9
			Feeding	Experimental	47.9 ± 55.4
				Control	0 ± 0
			Unknown	Experimental	1.3 ± 2.5
				Control	15.9 ± 31.8
		Medium (12)	Immobile	Experimental	25.4 ± 28.0
				Control	49.0 ± 37.8
			Mobile	Experimental	34.7 ± 31.2
				Control	35.0 ± 27.5
			Contact Animal	Experimental	0.8 ± 2.0
				Control	0.8 ± 2.6
			Contact Stimulus	Experimental	0 ± 0
				Control	0 ± 0
			Feeding	Experimental	36.1 ± 40.8
				Control	0 ± 0
			Unknown	Experimental	3.5 ± 6.5
				Control	15.2 ± 28.8
		Large (4)	Immobile	Experimental	11.7 ±17.8
				Control	68.9 ± 15.5
			Mobile	Experimental	62.5 ± 40.8
				Control	26.8 ± 8.5
			Contact Animal	Experimental	0 ± 0
				Control	0 ± 0
			Contact Stimulus	Experimental	0 ± 0
				Control	0 ± 0
			Feeding	Experimental	23.8 ± 47.5
				Control	0 ± 0
			Unknown	Experimental	4.4 ± 6.2
				Control	4.4 ± 8.7
Hippasteria phrygiana	Cup Coral	Small (4)	Immobile	Experimental	49.1 ± 47.6
				Control	61.9 ± 22.8
			Mobile	Experimental	44.3 ± 44.2
				Control	38.1 ± 24.6
			Contact Animal	Experimental	2.2 ± 2.5
				Control	0 ± 0
			Contact Stimulus	Experimental	0 ± 0
				Control	0 ± 0
			Feeding	Experimental	1.1 ± 2.2
				Control	0 ± 0
			Unknown	Experimental	3.3 ± 4.2
				Control	0 ± 0
		Medium	Immobile	Experimental	38.3 ± 32.4

		(12)		Control	46.1 ± 36.7
			Mobile	Experimental	41.8 ± 30.5
				Control	41.8 ± 31.3
			Contact	Experimental	3.3 ± 5.9
			Animal	Control	10.6 ± 20.9
			Contact	Experimental	0 ± 0
			Stimulus	Control	0 ± 0
			Feeding	Experimental	15.6 ± 36.4
				Control	0 ± 0
			Unknown	Experimental	0.7 ± 2.5
				Control	1.5 ± 4.02
		Large (4)	Immobile	Experimental	48.5 ± 32.6
				Control	30.9 ± 32.4
			Mobile	Experimental	27.7 ± 16.0
				Control	66.7 ± 31.7
			Contact	Experimental	0 ± 0
			Animal	Control	1.2 ± 2.4
			Contact	Experimental	0 ± 0
			Stimulus	Control	0 ± 0
			Feeding	Experimental	23.9 ± 47.7
				Control	0 ± 0
			Unknown	Experimental	0 ± 0
				Control	0 ± 0
**Ceramaster granularis* + *Henricia lisa*	Sponge	*C. granularis* (2)	Immobile	Experimental	52.2 ± 24.6
				Control	15.2 ± 9.2
			Mobile	Experimental	43.5 ± 18.5
				Control	76.1 ± 9.2
			Contact	Experimental	0 ± 0
			Animal	Control	0 ± 0
			Contact	Experimental	0 ± 0
			Stimulus	Control	0 ± 0
			Feeding	Experimental	0 ± 0
				Control	0 ± 0
			Unknown	Experimental	4.4 ± 6.2
				Control	8.7 ± 0
		H. lisa (2)	Immobile	Experimental	0 ± 0
				Control	21.7 ± 30.7
			Mobile	Experimental	2.2 ± 3.1
				Control	58.7 ± 46.1
			Contact	Experimental	0 ± 0
			Animal	Control	0 ± 0
			Contact	Experimental	0 ± 0
			Stimulus	Control	0 ± 0
			Feeding	Experimental	97.8 ± 3.1
				Control	0 ± 0
			Unknown	Experimental	0 ± 0
				Control	19.6 ± 15.4
**Ceramaster granularis* + *Buccinum scalariforme*	Octopus	*C. granularis* (2)	Immobile	Experimental	0 ± 0
				Control	43.9 ± 49.8
			Mobile	Experimental	4.3 ± 0.1
				Control	34.3 ± 19.1
			Contact	Experimental	0 ± 0
			Animal	Control	4.4 ± 6.2
			Contact	Experimental	0 ± 0
			Stimulus	Control	0 ± 0
			Feeding	Experimental	95.7 ± 0.1

				Control	0 ± 0
			Unknown	Experimental	0 ± 0
				Control	17.4 ± 24.6
		B. scalariforme (2)	Immobile	Experimental	65.7 ± 19.1
				Control	47.6 ± 49.6
			Mobile	Experimental	34.3 ± 19.1
				Control	27.3 ± 26.3
			Contact	Experimental	0 ± 0
			Animal	Control	4.4 ± 6.2
			Contact	Experimental	0 ± 0
			Stimulus	Control	0 ± 0
			Feeding	Experimental	0 ± 0
				Control	0 ± 0
			Unknown	Experimental	0 ± 0
				Control	20.8 ± 29.5
Ceramaster granularis + *Henricia lisa* + *Buccinum scalariforme*	Octopus	*C. granularis* (4)	Immobile	Experimental	5.0 ± 7.1
				Control	29.1 ± 36.7
			Mobile	Experimental	36.3 ± 45.7
				Control	50.3 ± 31.8
			Contact	Experimental	1.3 ± 2.5
			Animal	Control	5.7 ± 8.6
			Contact	Experimental	0 ± 0
			Stimulus	Control	0 ± 0
			Feeding	Experimental	57.5 ± 43.5
				Control	0 ± 0
			Unknown	Experimental	0 ± 0
				Control	14.9 ± 23.8
		H. lisa (4)	Immobile	Experimental	0 ± 0
				Control	7.5 ± 15.0
			Mobile	Experimental	9.5 ± 8.5
				Control	50.8 ± 37.6
			Contact	Experimental	0 ± 0
			Animal	Control	2.4 ± 4.8
			Contact	Experimental	0 ± 0
			Stimulus	Control	23.9 ± 47.7
			Feeding	Experimental	69.2 ± 46.8
				Control	0 ± 0
			Unknown	Experimental	21.3 ± 42.5
				Control	15.5 ± 31.0
		B. scalariforme (4)	Immobile	Experimental	49.5 ± 38.2
				Control	38.8 ± 26.0
			Mobile	Experimental	42.1 ± 43.3
				Control	35.9 ± 9.9
			Contact	Experimental	0 ± 0
			Animal	Control	5.7 ± 8.6
			Contact	Experimental	0 ± 0
			Stimulus	Control	0 ± 0
			Feeding	Experimental	8.5 ± 11.3
				Control	0 ± 0
			Unknown	Experimental	0 ± 0
				Control	19.6 ± 24.3

*Indicates experimental trials with two replicates instead of four.

3.9.2 Supplementary Figures

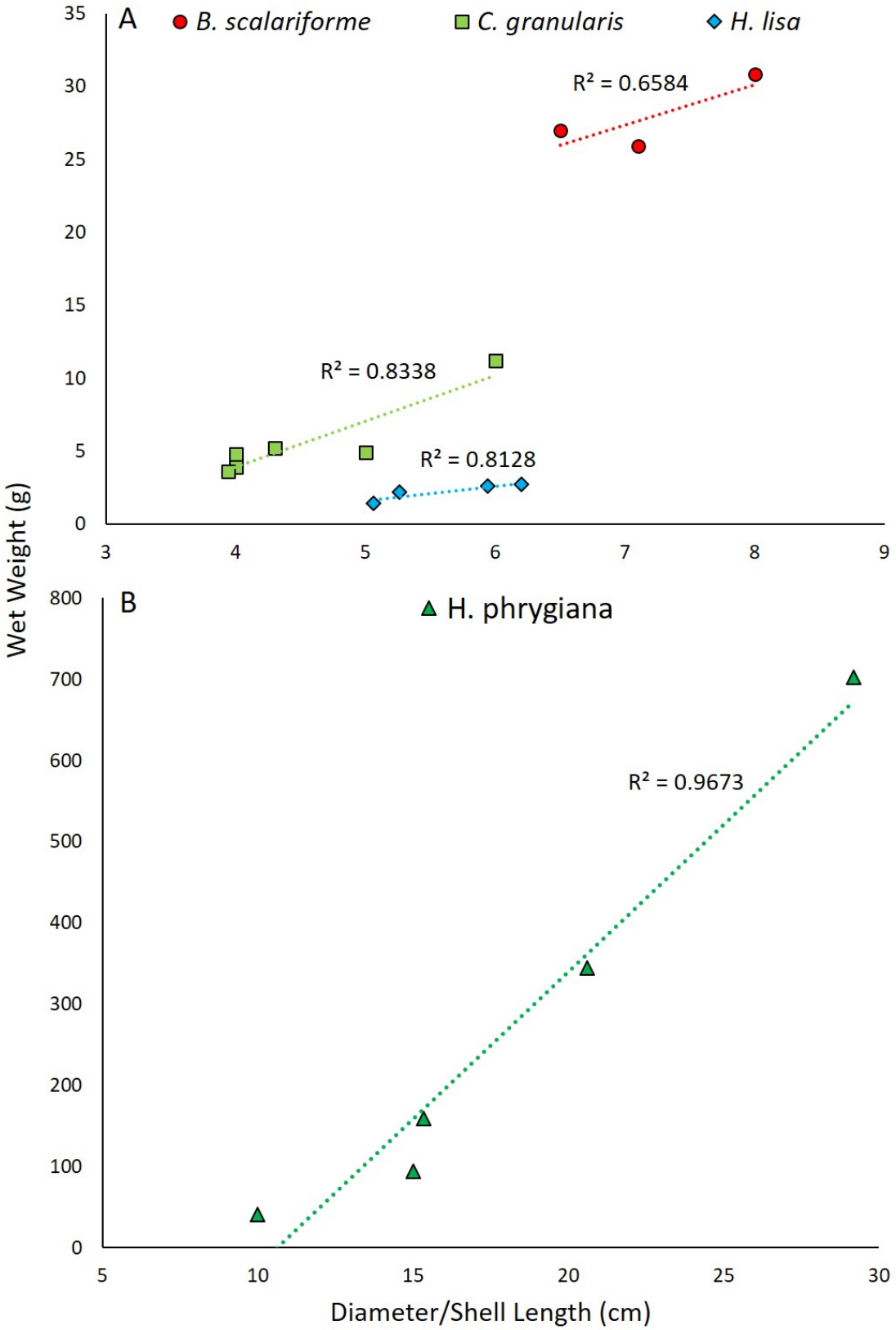

Figure S 3.1 (previous page) Animal wet weight (g) to diameter/shell length (cm) for (A) *Buccinum scalariforme*, *Ceramaster granularis*, *Henricia lisa*, and (B) *Hippasteria phrygiana* with R^2 values. Note the different X and Y scales in panels A and B. Results for *H. phrygiana* were graphed separately due to the very different body size scale of this species.

3.9.3 Supplementary Videos

Videos are available through Memorial University's research repository

Video S3.1: Small *C. granularis* wedging under a large *C. granularis*

Video S3.2: Small *C. granularis* blocking a large *C. granularis* and four small *C. granularis* cooperatively feeding

Video S3.3: Large *C. granularis* pushing small *C. granularis* off food

Video S3.4: Medium *H. phrygiana* pushing small *H. phrygiana* off food

Video S3.5: Large *H. phrygiana* skirting around small *H. phrygiana* to reach food

Video S3.6: *H. lisa* tapping food

Video S3.7: *H. lisa* traveling to food

Video S3.8: *B. scalariforme* approaching food

Video S3.9: *C. granularis* wedging under *H. lisa*

Video S3.10: *C. granularis* being bitten by polychaete

Video S3.11: *H. phrygiana* appearing agitated on food fall

Video S3.12: *H. lisa* showing dorsal body wall pulsing

Video S3.13: *H. lisa* tapping food fall

Video S3.14: Large *H. phrygiana* chasing away small *H. phrygiana* from food fall

Video S3.15: *B. scalariforme* pushing each other off food

Video S3.16: *H. phrygiana* harassing *B. scalariforme* at food fall

Chapter 4 General Conclusions

4.1 Thesis summary

In this thesis I used a combination of singleton feeding trials, multiple individual (conspecific and heterospecific) feeding trials, and simulated food fall experiments to assess the diet, locomotor and foraging behaviours, and competitive dynamics of four deep-sea benthic species commonly found in the Northwest Atlantic.

In Chapter 2, I showed that the diets of the focal species were more expansive than previously believed, perhaps because deep food-limited environments promote more generalist diets. This study lends support to the previously proposed hypothesis that the sea star *Ceramaster granularis* is a generalist with scavenging tendencies (Gale et al., 2013), feeding upon a wide array of food items, from sponges to carrion food falls. Also in line with the work of Gale et al. (2013), *Hippasteria phrygiana* reacted most quickly to the cup coral *Flabellum alabastrum* in the present study although this reaction was slowed slightly when competitors were present. However, carrion scavenging tendencies for this species were highlighted in the present study. While *Henricia lisa* is typically considered to be primarily a spongivore like other members of the genus *Henricia* (Mercier & Hamel, 2008; Robertson et al., 2017), and although *H. lisa* fed upon all deep-sea sponges offered, it also fed upon various types of carrion, a diet component that was previously unreported from *in situ* observations. The gastropod *Buccinum scalariforme* also fed upon various carrion, in line with the reported diets for other species in the genus *Buccinum* (Evans et al., 1996; Ilano et al., 2005; Aguzzi et al., 2012). The fine scale speed analysis of these slow-moving benthic species revealed a pulsing speed pattern that had previously been unreported for these taxa. Such movement patterns may be widespread in benthic marine taxa and may potentially be present in shallow-water species as well.

Chapter 3 investigated competitive dynamics between conspecifics and heterospecifics of the four focal species, in combinations of various numbers and sizes, during feeding trials and simulated food fall experiments (Figure 4.1). Multi-animal trials (of both conspecifics and heterospecifics) highlighted how species can modify their foraging strategies under different competitive scenarios. Plasticity was most apparent in *C. granularis*, which adjusted its response not only to the identity of potential competitors but also the size and number of competitors. The coordination of multiple smaller conspecifics acting to block a larger conspecific from reaching food is an intriguing behaviour that was previously unreported in sea stars. The largest species tested, *H. phrygiana*, was prompt to monopolize small food items; however, smaller individuals seemed unable to defend food resources against larger conspecifics. The small and relatively quick *H. lisa* adjusted its foraging strategy depending on the competitive environment, taking looping paths when alone and more direct paths when competitors were present. Finally, the whelk *B. scalariforme* competed with conspecifics for patches of food and displayed what could be interpreted as a kleptoparasitic relationship with *H. phrygiana,* which is likely one of its predators. My hypothesis that larger individuals would outcompete smaller individuals was not verified; large individuals of *H. phrygiana* outcompeted smaller conspecifics but large individuals of *C. granularis* only outcompete smaller conspecifics when those large individuals were not outnumbered by smaller, cooperating conspecifics. Likewise, my hypothesis that faster species would consistently outcompete slower species was also not proven; *H. lisa* is faster than *C. granularis*, however, the morphology of *C. granularis* appears to give it a competitive advantage, allowing it to push *H. lisa* off food items. In addition, *B. scalariforme* is faster than *H. phrygiana* but can be driven away from food items by *H. phrygiana* which displays potentially predatory behaviours towards it.

Together, the results from these two chapters show that what species *can* eat, and what they *do* eat, may be different. Ecological constraints and competitive dynamics may limit what food resources a given species or individual has access to. Competitive dynamics can have important impacts at the community and ecosystem levels (Menge & Menge, 1974; Buss, 1981; Schmid & Schaerer, 1981; Schmitt, 1987; Rogers et al., 2018; St-Pierre et al., 2018) and acknowledging these dynamics is critical to our understanding of ecosystem services and to the development of conservation plans (Danovaro et al., 2020). As anthropogenic impacts on the deep sea are anticipated to intensify in the future (Ramirez-Llodra et al., 2010; 2011; Mestre et al., 2014; Levin & Le Bris, 2015), increasing protection for these currently understudied ecosystems and species (Danovaro et al., 2017) will be necessary in order to preserve their functions and biodiversity.

4.2 Future directions

Species-specific experimental studies allow us to determine what a species finds palatable and how it forages undisturbed, while studies involving multiple conspecifics or heterospecifics increases behavioural complexity and more accurately reflects the natural environment. In addition, using well acclimated individuals in darkened, cold-water, flow-through settings can help capture more natural behaviours than studies that take place shortly after collection and/or in brightly lighted settings. Moving forward, and assuming that the logistical challenges can be overcome, experimental studies would benefit from creating more complex experimental arenas for video analysis of locomotor and behavioural patterns (as opposed to the smooth flat ones used here), offering a wider variety of food types (e.g. bacterial mats, polychaetes, marine mammal carcasses), testing a broader diversity of species (e.g. polychaetes, crustaceans, fishes) and testing the sensory detection ranges of these species. In

addition, a higher number of replicates would be beneficial to more accurately determine behavioural and statistical trends. The present study highlights how food fall or baited camera experiments conducted *in situ* may benefit from using infrared lights and cameras to avoid potential light-associated biases and disruptions. Importantly, the design of such *in situ* experiments should not exclude species like sea stars and gastropods (e.g. due to suspended bait or low video resolution). All four species in this study showed a willingness to feed upon both types of simulated food falls; therefore, they likely have an impact on the competitive dynamics surrounding these punctual food inputs in the deep sea, and ultimately on how nutrients cycle through their food-limited environment. The baseline information in this study will hopefully provide a starting point for researchers who wish to investigate these species more in-depth in the future, and the behavioural information may help contextualize *in situ* observations of these, or similar, species.

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4.4 Figures

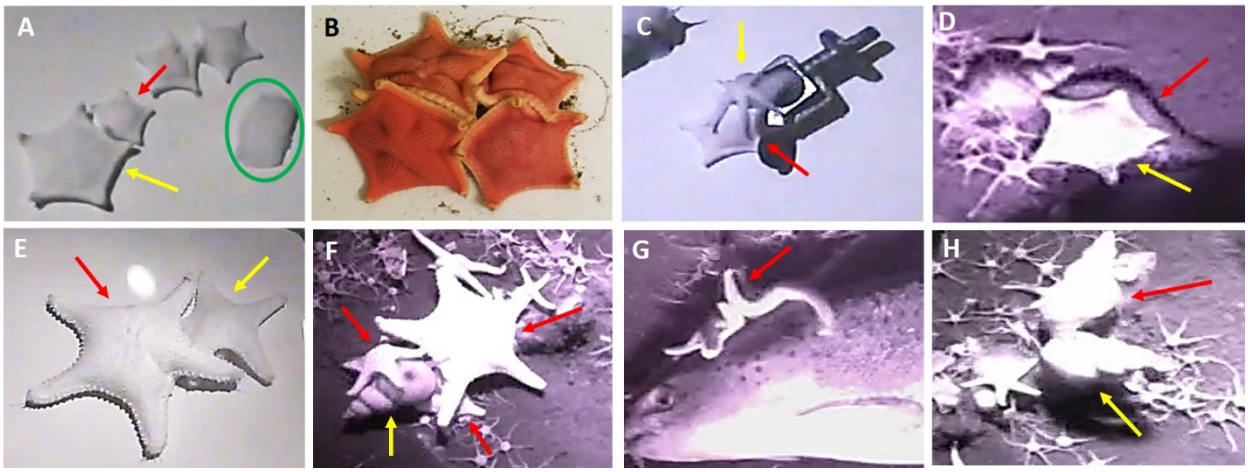

Figure 4.1 Some behaviours of interest from this study: (A) a small individual of *Ceramaster granularis* (red arrow) blocking a large conspecific (yellow arrow) from accessing food (green circle). (B) Similar sized conspecifics of *C. granularis* cooperatively feeding upon a food item after successfully repelling a large conspecific. (C) *C. granularis* (red arrow) wedging under *H. lisa* (yellow arrow) to access food. (D) An unidentified infaunal polychaete (red arrow) biting *C. granularis* (yellow arrow) during a simulated food fall in a mesocosm. (E) A large individual of *Hippasteria phrygiana* (red arrow) pushing a smaller conspecific (yellow arrow) off of a food item. (F) Three individuals of *H. phrygiana* (red arrows) of various sizes harassing *Buccinum scalariforme* (yellow arrow) during a simulated food fall in a mesocosm. (G) *H. lisa* with an arm raised (red arrow) to engage in tapping behaviour on a simulated food fall in a mesocosm. (H) *B. scalariforme* (red arrow) approaching and pushing a conspecific (yellow arrow) that was feeding upon a simulated food fall in a mesocosm.